

THE CONNECTIVITY FINGERPRINTS OF THE FRONTAL EYE FIELD AND THE INFERIOR FRONTAL JUNCTION

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ABSTRACT

Within the prefrontal cortex, the frontal eye field (FEF) and the inferior frontal junction (IFJ) are crucial regions that mediate attention, working memory, and cognitive control functions. I comprehensively reviewed the neuroimaging evidence on these regions, suggesting that they are specialized in the control of spatial versus non-spatial visual processing, respectively, and hypothesized that their connectivity fingerprints might underlie these roles.

To accurately infer the localization of these regions in standard space, I carried out an activation likelihood estimation (ALE) fMRI meta-analysis using tasks that reliably engage these regions. Prosaccade and antisaccade tasks were included in the FEF sample, whereas oddball/attention, n-back, Stroop and task-switching experiments were included in the IFJ sample ($n = 35$ and 32 , respectively). The ALE technique revealed the strongest convergence of activations at the junctions of the superior precentral sulcus and superior frontal sulcus for the FEF, and the inferior precentral sulcus and inferior frontal sulcus for the IFJ. I employed the resulting ALE peaks to perform a meta-analytic connectivity modeling analysis to uncover their whole-brain fMRI coactivations and decoded these patterns to infer significant associations with behavioral domains.

The ALE peaks from a subsample of the previous meta-analysis were used to analyze 3T diffusion MRI data released by the Human Connectome Project from 56 unrelated subjects. Using a surface-based probabilistic tractography approach, I tracked streamlines ipsilaterally from the FEF and IFJ to regions of the dorsal and ventral visual streams on the native white matter surface parcellated using the atlas by Glasser et al. (2016). By contrasting their connectivity likelihood, I found predominant structural connectivity from FEF to regions of the dorsal visual stream (particularly in the left hemisphere) compared to the IFJ, and conversely, predominant structural connectivity from the IFJ to regions of the ventral visual stream compared to the FEF. These results were replicated when accounting for the distance between FEF, IFJ, and the target regions.

The connectivity fingerprints of the FEF and IFJ provide converging evidence of their specialization in the control of spatial vs non-spatial processing, which is mediated by long-range white matter association pathways. The results presented in this dissertation overall support the view that the two-visual stream architecture extends to the human prefrontal cortex, as was originally hypothesized in the macaque based on tract tracing and neurophysiological evidence.

Chapter 1

Introduction

1.1 | THE PREFRONTAL CORTEX

Of the four lobes of the human cerebral cortex, the frontal lobe is likely the least understood. From an anatomical point of view, it includes all the regions anterior to the central sulcus and the lateral sulcus. We can distinguish two parts of the frontal lobe, namely the skeletomotor area and the prefrontal cortex (PFC; Donahue et al., 2018; McLaughlin & Malloy, 2018). The PFC is in turn divided into a lateral, medial and orbital portion (McLaughlin & Malloy, 2018). While the term PFC was coined and already used by neuroscience pioneers of the XIX century such as David Ferrier (Ferrier & Yeo, 1884), the first influential definition of the PFC was proposed by Brodmann (1909) based on cytoarchitectonic criteria. According to Brodmann's definition, the PFC includes all the areas of the frontal cortex that are characterized by a well-developed layer IV (referred to as granular or eulaminate cortex; McLaughlin & Malloy, 2018). Layer IV is typically considered an input layer that receives feedforward connections, and it is primarily composed of stellate cells and, to a lesser extent, of pyramidal cells. Brodmann's definition largely contributed to framing the debate on whether non-human primates and other mammals possess a PFC (Carlén, 2017; Preuss & Wise, 2022). As most mammals do not have a frontal granular cortex, this criterion seemed to exclude this possibility. Following this influential definition, the second one that came to perhaps implicitly dominate the field for the past 70 years was proposed by Rose and Woolsey (1948; Carlén, 2017). They observed that the frontal lobe is the only part of the cortex that receives projections from the mediodorsal nucleus of the thalamus. This nucleus appears to be essential for learning, decision-making, and executive functions (Mitchell, 2015). In the monkey, these thalamic projections are broadly segregated based on the three sectors of this nucleus: the parvocellular sector projects to the orbital portion of the frontal cortex, the magnocellular sector to the lateral frontal cortex, and the multiform sector to the posterior lateral frontal cortex near the arcuate sulcus (McLaughlin & Malloy, 2018; see Mitchell, 2015, for a finer distinction and wiring diagrams).

Since other mammals also had areas receiving these kinds of thalamic projections, this definition effectively opened up the field for cross-species investigation of the PFC, and prefrontal areas were identified in the macaque, rats, and in mice (Carlén, 2017). Clearly, however, there was more to this picture, as the mediodorsal thalamus did not project exclusively to the PFC, and other thalamic structures did so too, so this criterion should be regarded at best as a useful approximation. At present, not only does the field currently lack a widely accepted definition of the PFC, but the interest in identifying homologies in regions of the PFC adds further complexity to this question. This debate has in fact recently been sparked again by the possibility of investigating the PFC in animal models that are investigated using recently developed cutting-edge genetic techniques (Carlén, 2017).

I will come back to the important question of homologies between species in the following chapter of this dissertation, but I will for now leave aside comparative issues to focus on the human PFC. As definitions tend to stick, Brodmann's influential idea of the PFC as the granular frontal cortex was directly imported into the emerging neuroimaging techniques by being incorporated in the first stereotaxic atlas by Talairach and Turnoux (1988; Petrides, 2005). A careful examination of the cytoarchitecture of the lateral PFC

however revealed that layer IV is not equally present across the PFC, but that instead, some regions (especially in the posterior aspect) lack a well-developed layer IV, hence being referred to as dysgranular (Petrides & Pandya, 1999, 2002). These correspond to the premotor and motor areas of the PFC. Hence, it is tempting to adopt a simple negative definition of the PFC as every part of the cortex excluding premotor and motor areas (Chafee & Heilbronner, 2022). The transition from dysgranular to granular organization however emerges gradually and is smooth rather than constituting a sharp boundary (Geyer, 2004). While these considerations on the architecture and connectivity of the PFC are certainly important, a definition of the exact boundaries of the PFC will likely require the development of appropriate quantitative methods to measure and interpret the structural properties of the cortex by combining multiple imaging modalities (see for example Donahue et al., 2018 for a recent morphometric comparative analysis). For the scope of the present dissertation, these highlight two important factors to consider for a useful working definition of the PFC. First, cytoarchitecture seems an important guiding criterion that however ultimately needs to be coupled with function, consistent with the evidence that the PFC is ultimately responsible for the control of goal-driven behaviors that do not depend on present sensory stimulation (Fuster, 2001; Goldman-Rakic, 1996). Second, the connectional criterion (with the dorsomedial thalamus; Rose & Woolsey, 1948) suggests that the PFC (and its regions) may be best defined based on its broader intrinsic and extrinsic connectivity patterns (Fuster, 2001). I will expand on these two points in the following sections.

1.2 | FUNCTION OF THE PREFRONTAL CORTEX

In contemporary cognitive neuroscience, the functions thought to be mediated by the PFC are a growing number and haven't been yet summarized in a unitary framework (Szczepanski & Knight, 2014). In the clinical literature, they are tentatively grouped under the umbrella term of executive functions, which include voluntary attention, working memory, motivation, language production, planning, decision-making, inhibition, shifting and updating the task set, and others (Chafee & Heilbronner, 2022; reviewed in Szczepanski & Knight, 2014). Early brain lesions and stimulation studies were instrumental in advancing the notion that a localizationist approach can be fruitfully applied to study the PFC but were primarily limited by the fact that the extent and anatomical specificity of the lesions couldn't be easily controlled and determined (Luria, 1966; Szczepanski & Knight, 2014). This led many prominent researchers that carried out experimental ablations removing large portions of the frontal lobe to somewhat prematurely draw the conclusion that this lobe was cognitively silent (Szczepanski & Knight, 2014). In part due to the inconclusive nature of these previous results, much of the PFC was and in part still remains *terra incognita* (Casanova & Opris, 2015).

The most crucial breakthroughs in our understanding of the PFC can be traced back to the 1970-1980s when two prominent scientists started their respective investigations (Chafee & Heilbronner, 2022). Fuster and Alexander (1971) recorded single-unit responses in the principal sulcus of the macaque in a delayed match to sample task, showing evidence of sustained responses during the delay period in these neural populations. By bridging the duration between the presentation of the cue and the response period, the activity of these

prefrontal neurons provided a first elegant demonstration of a potential neural correlate of working memory processes (Fuster, 2001). In a later series of studies, Patricia Goldman-Rakic and colleagues showed that this activity was related to the type of information stored in working memory (e.g., the spatial location of a remembered item; Funahashi et al., 1989; reviewed in Goldman-Rakic, 1996). These ideas have proven to be extremely influential in the inception of neuroimaging methods, particularly in early positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies. Abundant evidence has now accumulated on the role of specific regions in sustained activity in the delay period in top-down attention and working memory paradigms (Corbetta & Shulman, 2002; Curtis & Sprague, 2019; Serences, 2016). In particular, fMRI studies showed that activity in several regions of the lateral PFC remains elevated throughout the delay period (Sreenivasan et al. 2014; Wager & Smith, 2003). Moreover, it became possible to decode if there is information carried by these activation patterns using multivariate pattern analysis (MVPA; for reviews see Haynes & Rees, 2005; Christophel et al. 2017; Curtis & Sprague, 2019). Although this evidence suggests that these regions are implicated in working memory processes, it remains to be elucidated how these regions interact with each other and the specific mechanisms that they mediate. In the lateral PFC, the same set of regions may be activated across different tasks. That seems to go against a strict modular interpretation where each region performs a specialized role. This evidence was at the foundation of the multiple demand hypothesis (Duncan, 2010) which posits that prefrontal regions can mediate goal-driven behavior in a domain-general fashion.

Without delving deeper into the debate between modular and domain-general views on the PFC, I would like to draw some implications from the points discussed in this section. First of all, it is clearly challenging to assign cognitive processes that share a significant degree of overlap to specific regions of the PFC. For instance, attention and working memory both require the active maintenance of representations to influence subsequent behavior and have thus been suggested to rely on shared neural substrates, including multiple PFC regions (Chun et al., 2011; Gazzaley & Nobre, 2012; van Ede & Nobre, 2023). A similar line of reasoning may arguably apply to several other functions that are referred to as executive and exemplifies the more general problems of relating psychological constructs to the underlying neural correlates (Poldrack, 2006; Turner, 2016), and of testing models of cognition using neuroimaging data (Coltheart, 2006). Overall, this context poses a significant challenge when trying to understand the organization of the PFC and its functional specialization. Even in the case of areas that are thought to be highly specialized, such as, taking a famous example, Broca's area, referring to it as a center crucial for language production would only capture part of its role (Friederici, 2011). Its functions are furthermore dependent on the connections between this area and the rest of the language network, hence these cannot be strictly speaking localized within Broca's area alone (de Schotten & Forkel, 2022).

Instead of labeling each PFC region using psychological terminology (which as in the example above would come with a rather strong assumption of modularity), Passingham and Lau (2022) suggested reframing the problem and taking a more fruitful path by first looking at each subdivision of the PFC and trying to understand its function by carefully examining

its connections. It is in fact the set of inputs and outputs that each region possesses that ultimately constrain the kind of processes that it is able to perform (Passingham et al., 2002). I would like to suggest that this proposal presents several great advantages. First of all, the PFC is one of the most densely interconnected parts of the human brain (Barrett et al., 2020), and there is already robust evidence of the fact that each region possesses a distinctive pattern of connectivity, both intrinsically and with the rest of the brain (Croxson et al., 2005). Secondly, our arguably greater understanding of sensory function (particularly vision) in the brain can constrain our models of the kind of control processes mediated by PFC regions based on its communication with posterior regions. Finally, this proposal effectively circumvents any strict form of localizationism in favor of the view that, although each region of the PFC may be specialized for some function, it doesn't work in isolation, but needs to communicate with other regions to integrate information and guide behavior (Fuster, 2001). Understanding the function of the PFC from a network perspective (Menon & D'Esposito, 2022) opens up the possibility of applying new computational techniques that have recently emerged from the field of brain connectomics (Haber et al., 2022; Sporns et al., 2005; Van Essen et al., 2013). A caveat to this approach is that while it can improve our understanding of general principles of communication of the PFC with other systems, it needs to be complemented by advances in cognitive and computational models of the functions investigated. As an example, suppose that researchers are interested in understanding the neural mechanisms of visual attention using a normalization model (Maunsell 2015) with feedback components. In this scenario, they may start looking for the sources of these feedback signals that affect processing in visual areas in higher regions in the hierarchy. If for instance area x in the PFC doesn't have connections (either direct or indirect) with the visual area where attentional modulations are measured, then it would become an unlikely candidate to implement the feedback components under the model in its simplest form. I would now like to introduce some of the theories proposed to describe how the PFC is organized from a more general point of view to further clarify how the connectivity aspect may play into this organization.

1.3 | GRADIENTS IN THE PREFRONTAL CORTEX

The organization of the PFC has been mainly described by principles that follow the three topological axes: a rostral-caudal, a dorso-ventral and a medial-lateral (Badre & D'Esposito, 2009; O'Reilly, 2010). These axes delineate overlapping gradients that span the entire PFC. I will review each gradient separately below. Although these organizational principles are quite broad, they have been able to accommodate various sources of evidence from neuroimaging studies. The rostral-caudal axis delineates a gradient along which each region encodes information at different levels of abstraction (Koechlin et al., 2003). More specifically, it posits a hierarchy in information processing from sensory (in caudal regions) to progressively more abstract coding (in rostral ones). This hypothesis has mainly received support from fMRI studies performing effective connectivity analyses (Nee & D'Esposito, 2016), which refers to a family of techniques that allow the modeling of causal interactions between brain regions. To date, it still remains to be elucidated whether the abstraction level can be defined based on temporal proximity (i.e., responses dependent on environmental cues are less abstract when closer in time) or relational complexity (i.e., the number of features

that need to be integrated to respond; Nee et al., 2014). Previous studies that manipulated these variables showed that they altered the ensuing gradient in a task-dependent way and related to different anatomical subdivisions of the PFC, leading to the suggestion that this gradient should not be conceptualized as unidimensional (Badre & Nee 2018).

A second crucial axis is the dorso-ventral, which is the primary focus of this dissertation, relating to the distinction between the ‘what’ and ‘where’ (or ‘how’; Goodale & Milner, 1992) visual streams. One of the core foundations of the neuroscience of vision is the theory that, similar to the non-human primate visual system (Mishkin et al., 1983; Kravitz et al., 2011, 2013), the human brain processes visual information along two segregated visual streams, a dorsal and ventral one (Goodale & Milner, 1992). In the dorsal stream, areas are specialized to process spatial information that governs the execution of specific actions (i.e., eye movements, reaching and grasping), and possess a topographic visual organization (Kravitz et al., 2011; Wang et al., 2015). In the ventral stream instead, the recurrent processing that enables object recognition takes place (Kravitz et al., 2013). While this theory underwent some adaptations during the past 30 years, for example highlighting the interactions and crosstalk between these two pathways at various levels of the visual processing hierarchy (Cloutman, 2013; de Haan et al., 2018), it remains a fundamental pillar in visual neuroscience. In working within such a framework, it started to become apparent to researchers using invasive recordings that the macaque PFC was organized along similar principles. This led Goldman-Rakic and others to posit that the dual visual stream architecture extended to the PFC (Goldman-Rakic, 1996; Romanski, 2004; Wilson et al., 1993), a hypothesis which is supported by decades of tract-tracing (Kravitz et al., 2013; Yeterian et al., 2012) and mounting neurophysiological evidence in the macaque (Constantinidis & Qi, 2018; Martinez-Trujillo, 2022). Importantly, this hypothesis also received support from the human neuroimaging literature (O’Reilly, 2010) showing that it can be applied to effectively understand the function of posterior-lateral PFC areas (Chan, 2013). Finally, along the medio-lateral axis, we find a gradient that goes from areas that respond to emotional/motivational (‘hot’) factors to lateral areas that mediate purely sensory and cognitive (‘cold’) processes (O’Reilly, 2010). More concretely, medial areas tend to be involved in contexts of decision-making under uncertainty, where significant gains or losses can be expected, such as in the Iowa gambling task widely used in the neuropsychological literature (Brevers et al. 2013). It is important to underline that these organizational principles intersect with each other (Nee & D’Esposito, 2016; O’Reilly, 2010) and that we can therefore start to already infer the role of each PFC region based on its position along these three gradients. Even though this offers only an overview of PFC function, which leaves us with the need to specify more detailed coordinates for functional specialization, this helps to break down the problem of attentional and cognitive control (the ‘homunculus’ problem; Nobre, 2001; Passingham & Lau, 2022) in progressively smaller chunks that can be tackled experimentally. From this perspective, regions of posterior-lateral PFC should process information encoded in a format that is still likely a sensory one (i.e., visual), although it can be flexibly adjusted to a more abstract one, and perform complex cognitive processes close to the motor output in the cognitive processing cascade. The dorsal aspect of the posterior-lateral PFC mediates the processing of spatial information and action control, and

its ventral aspect mediates the processing of information related to object identity and task rules (Passingham & Lau, 2022). I discuss these aspects in the following section by drawing on comparative and human neuroimaging evidence.

1.4 | THE POSTERIOR-LATERAL PREFRONTAL CORTEX IN MACAQUES AND HUMANS

Invasive recordings allowed researchers to access a wealth of information about the function of the posterior-lateral PFC in the macaque (Martinez-Trujillo, 2022). This part of the PFC, localized near and anterior to the arcuate sulcus, is crucial for selecting relevant stimuli in the environment, oculomotor control and maintaining information in an active state to guide behavior (Schall, 2015). The mechanisms of visual selection have been extensively characterized at the behavioral and neural level (Carrasco, 2011; Desimone & Duncan, 1995; Kastner & Ungerleider, 2001; Moore & Zirnzak, 2017) and several computational models have been put forward (Heinzle et al., 2007; Itti & Koch, 2001; Maunsell, 2015). This combination of detailed information about behavioral outcomes, cognitive mechanisms, computational modeling and neural activity gives us a unique window into how the PFC exerts top-down control and may be used as a model in studying other functions of this structure of the brain. As a representative seminal study, Moore and Armstrong (2003) recorded from the frontal eye field (FEF), a region localized in the arcuate sulcus of the macaque (Schall, 2015), while the animals were fixating and oriented bars were presented. It is well established that when the animals attend a target that is in their receptive field (RF), these neurons will increase their firing rates (Maunsell, 2015). When the authors applied microstimulation on the FEF and recorded single-neuron activity in area V4, the activity increased in V4 RFs corresponding to the stimulated location within FEF. The effects of this stimulation mimicked the increase in the firing rate observed in covert attention tasks. Importantly, these increases were observed regardless of the fact that the stimulus was behaviorally relevant and critically depended on the direction of the saccade encoded by the FEF neurons (Moore & Armstrong, 2003). These results elegantly bridge the behavioral and neural levels by using the direct causal manipulation of brain activity, and together with subsequent studies provide an excellent working model of how top-down attention is implemented in the macaque PFC (reviewed in Moore & Zirnzak, 2017).

In contrast to these invasive approaches, neuroimaging methods are due to their non-invasive nature only equipped to measure the combined activity of several thousands of neurons, directly or indirectly, and with different degrees of spatial and temporal resolution (Gross, 2019). While these methods enabled measuring ongoing neural activity in humans at the whole-brain level, their ability to provide insights into the mechanisms of higher cognitive functions and the way they map onto specific structures of the PFC has been limited by several factors. For the purposes of this dissertation, the most critical ones are the low sample size used in previous studies (Button et al., 2013), the large interindividual variability that characterizes the PFC (Juch et al., 2005), which complicates establishing adequate anatomical specificity, and finally, questions regarding the reproducibility of the results particularly in fMRI research (Botvinik-Nezer et al., 2020; Eklund et al., 2016).

Countering these limitations is the fact that we now have access to a wealth of neuroimaging data, which can be leveraged to perform systematic quantitative meta-analyses (Fox et al., 2014) or used to carry out analyses in large datasets thanks to the advances in computational techniques to map the human connectome that originated in the past decade (Van Essen et al., 2013). Studies combining neuroimaging methods (i.e., diffusion MRI, resting-state fMRI) to perform macaque-to-human cross-species comparison have once again supported the fact that the macaque is an excellent animal model to understand the organization and connectivity of the PFC (Neubert et al., 2014; Sallet et al., 2013). Overall, these innovations led to a greater understanding of the organization of the PFC and the brain networks it participates in (Cole & Schneider, 2007; Corbetta & Shulman, 2002; Menon & D’Esposito, 2022). Looking at the PFC through the lens of these network models can help bridge the gap between a strict modular interpretation of the function of the PFC and domain-general views (Assem et al., 2020; Duncan, 2010) by positing the existence of specialized prefrontal regions that, through flexible communication with posterior regions, achieve efficient performance according to the stimulus domain and the task demands (Baldauf & Desimone, 2014; Fuster, 2001).

In this dissertation, I aim to show how neuroimaging and computational methods to infer brain connectivity can allow us to further understand the functional specialization of two regions of the posterior-lateral PFC. In particular, I will start by comprehensively reviewing the literature on the structure, function and connectivity of the Frontal Eye Field (FEF) and the Inferior Frontal Junction (IFJ), suggesting that they may perform complementary dissociated roles across attention, working memory and cognitive control functions. In the second chapter, I will present the results of a coordinate-based meta-analysis that was carried out to accurately infer the localization of these regions in standard space and overcome some of the limitations of previous meta-analyses. Having localized these regions, this chapter also examines their coactivation patterns across the whole brain. Finally, in the third chapter, I will exploit the information provided by diffusion MRI to infer the structural connectivity of these regions in a large dataset of healthy subjects (Van Essen et al., 2013). Overall, the results presented in this dissertation support the hypothesis that the functional specialization of the FEF and IFJ critically depends on their connectivity fingerprints (Osher et al., 2016; Passingham et al., 2002; Saygin et al., 2012).

Chapter 2

Structure, function and connectivity fingerprints of the frontal eye field versus the inferior frontal junction: A comprehensive comparison

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2.1 | INTRODUCTION

It is remarkable to what extent primates have evolved the cognitive faculties that allow their behaviour to be guided not only by their immediate surroundings and environment but also by their future goals and action plans (Fuster, 2001). The successful orchestration of these goal-driven behaviours requires the adaptive coding of contextual information (Duncan, 2001), and the integration of this information in order to bias processing in other brain areas (Barceló et al., 2000) and to finally map sensory input into coherent behavioural sequences (Miller & Cohen, 2001). Our ability to prioritize important sensory information (a function named selective attention; Carrasco, 2011; Posner, 1980) arguably plays a crucial role in all the former processes. Visual selection, for example, is thought to be guided top-down by ‘attentional templates’ (Desimone & Duncan, 1995), which can assume highly divergent representational formats, for example, in the form of spatial as opposed to feature- and object-based attention (hereafter referred to spatial and non-spatial attention/selection; Carrasco, 2011; see also Moore & Zirnsak, 2015). In a typical everyday life situation, we may know how the object we are searching for looks like (e.g., our bicycle), but its current location (if we forgot where we parked it). Conversely, we often remember an objects’ location, but due to the environmental clutter, we may not recognize it until we focus our spatial attention there. In both instances, it is the specific ‘attentional template’ that we adopt to guide our search that boosts the representation of the object’s location, or its identity, allowing us to select it and move on to our next goal. A fundamental question in cognitive neuroscience is, therefore, where and how attentional priorities are computed in the primate brain (Desimone & Duncan, 1995; Itti & Koch, 2001), and how spatial and non-spatial selective mechanisms interact to enable flexible and efficient goal-driven behaviour (O’Reilly, 2010; Rao et al., 1997).

The prefrontal cortex (PFC) has long been recognized to be crucially involved in many aspects of such complex, organized behaviour in non-human and human primates (Fuster & Alexander, 1971; Luria, 1966; Norman & Shallice, 1986; Rainer et al., 1998). In the past decades, several investigators, most notably Patricia S. Goldman-Rakic, advanced the hypothesis that also the PFC can be segregated into functionally distinct domains (Goldman-Rakic, 1996; Romanski, 2004; Wilson et al., 1993). In particular, what motivated Goldman-Rakic to posit the domain-specific organization of the PFC was the observation of substantial differences in the selectivity of neurons (Wilson et al., 1993), as well as their anatomical connectivity patterns (reviewed in Goldman-Rakic, 1996). Together, these patterns of selectivity and connectivity suggested that the posterior lateral PFC (plPFC) contained two segregated regions that belonged to the global dorsal and the ventral visual streams (Goodale & Milner, 1992; Mishkin et al., 1983), and which predominantly encoded spatial and object information, respectively (Goldman-Rakic, 1996; Scalaidhe et al., 1997, 1999; Wilson et al., 1993). More recently, this framework was further supported by mounting evidence in primates (Bichot et al., 2015, 2019; Constantinidis & Qi, 2018; Meyer et al., 2007, 2011; Riley et al., 2017; Schwedhelm et al., 2020) and was expanded thanks to neuroimaging methods in humans, in the context of studies focusing on understanding how the PFC maintains top-down control over visual selection and encodes behaviourally relevant

stimuli in various experimental tasks (Baldauf & Desimone, 2014; Chan, 2013; O'Reilly, 2010; Serences, 2016).

This review will focus on the organization of the plPFC in humans. In particular, we will compare in detail two regions that are implicated in visual attention, working memory and cognitive control, namely, the frontal eye field (FEF) and the inferior frontal junction (IFJ). We would therefore like to stress that the goal of this paper is not to provide a systematic review of FEF and IFJ per se, as these are already available elsewhere (the FEF has been reviewed extensively in Petit & Pouget, 2019; Vernet et al., 2014; the IFJ was reviewed in Brass et al., 2005). Rather, in the following, our goal will be to highlight the properties that reveal crucial differences in the structure, function and connectivity of these two areas and to systematically compare them to uncover their functional specialization. In the last decade, research has been able to successfully disentangle the specific contribution of both of these areas to visual attention and working memory through the careful combination of neuroimaging methods (functional magnetic resonance imaging [fMRI] and magnetoencephalography [MEG]) with more sophisticated data analysis tools (i.e., multivariate pattern analysis [MVPA], Haxby et al., 2001; and functional and effective connectivity metrics, e.g., Baldauf & Desimone, 2014; Nee & D'Esposito, 2016; Sneve et al., 2013; Vossel et al., 2012; Wen et al., 2012; Zhang et al., 2018). Therefore, we aim to understand how the structure, function and connectivity fingerprints of the FEF and the IFJ constrain and shape their role in these cognitive functions and the underlying brain networks (Table 1).

Table 1 List of the main abbreviations used in the text and figures

Abbreviation	Full name	Abbreviation	Full name
ALE	Activation Likelihood Estimation	MFG	Middle Frontal Gyrus
BA	Brodmann Area	MMP1	Multi-Modal Parcellation 1.0
DAN	Dorsal Attention Network	MVPA	Multivariate Pattern Analysis
dMRI	Diffusion Magnetic Resonance Imaging	PCS	Precentral Sulcus
FEF	Frontal Eye Field	PFC	Prefrontal Cortex
FFA	Fusiform Face Area	PPA	Parahippocampal Place Area
IFG	Inferior Frontal Gyrus	SLF	Superior Longitudinal Fasciculus
IFJ	Inferior Frontal Junction	SFS	Superior Frontal Sulcus
IFS	Inferior Frontal Sulcus	SPL	Superior Parietal Lobule
IPS	Intraparietal Sulcus	TPJ	Temporo-Parietal Junction
MACM	Meta-Analytic Connectivity Modeling	VAN	Ventral Attention Network

According to the classic definition, these three criteria (structure, function and connectivity) define the concept of a cortical region, along with topographic (i.e., somatotopic or retinotopic) organization (Eickhoff, Constable, & Yeo, 2018). However, the latter is generally deemed less important beyond unimodal sensory cortices (Eickhoff, Constable, & Yeo, 2018). In contrast to early visual areas, where all these cortical features are generally well aligned, and inter-individual differences are small, leading to a reliable way to parcel the underlying brain structures (Abdollahi et al., 2014; Sereno et al., 1995), in the PFC

studies show that the alignment between cortical features becomes less apparent, and even the relative spatial arrangement of brain areas can sometimes vary substantially between individuals (Eickhoff, Yeo, & Genon, 2018). Thus, to understand the modular organization of the PFC, a multimodal approach capable of combining information about all the most relevant cortical properties becomes crucial (Glasser et al., 2016; Van Essen et al., 2019). Another relevant concept in the present context is the idea that the function of a brain region is heavily constrained by its intrinsic and extrinsic connectivity fingerprints (Passingham et al., 2002). Indeed, only by describing the connectivity fingerprints of each region, we are able to fully understand the most relevant aspects of functional specialization of the regions in the PFC, and in particular, those that are fundamentally underlaid by the differential selectivity of their neural populations to specific sensory inputs. Together, these two principles will guide the organization of this review in three main sections: the first, in which we will compare the structure of FEF and IFJ, the second, in which we will compare the function of FEF and IFJ, and a final third section, in which we will describe and contrast their connectivity fingerprints.

1.1 | History and definition

The discovery of a brain area involved in the oculomotor aspects of behaviour in the monkey dates back to the work of the Scottish neurophysiologist David E. Ferrier in the last half of the 19th century. He reported that: ‘In the superior frontal convolution, in advance of the centre, for certain forward movements of the arm, as well as in the corresponding part of the middle frontal convolution, are areas, stimulation of which causes lateral (crossed) movements of the head and eyes and dilatation of the pupils’ (Ferrier, 1875; cited in Vernet et al., 2014). Thus, the way the FEF has been labelled directly reflects its hypothesized oculomotor function, a fact that may have contributed to obscure the large discrepancy between the way this region has been traditionally mapped in primates (i.e., by microstimulation techniques; Bruce et al., 1985) and the way it was localized in early neuroimaging studies, and consequently ‘translated’ into the human brain’s taxonomic language (Paus, 1996; Petit & Pouget, 2019). To date, the FEF has been the subject of hundreds of studies both in monkeys and in humans (reviewed in Petit & Pouget, 2019, Tehovnik et al., 2000, and Vernet et al., 2014). Despite the considerable efforts of the neuroscientific community to characterize the FEF, this region’s structure, function and connectivity in humans are often debated and are not yet fully understood. The IFJ, in contrast, came under the spotlight of the neuroscientific community only much more recently. According to Sundermann and Pfeleiderer (2012), although this region has been the object of many neuroimaging studies investigating various components of cognitive control, task-switching and working memory, researchers have often missed reporting the IFJ as a segregated brain region. The IFJ was first described with the current label in a series of influential studies by Brass, Derrfuss, von Cramon and colleagues (Brass & von Cramon, 2002, 2004; Derrfuss et al., 2004, 2005; see also Bunge et al., 2003, and Sylvester et al., 2003, for a converging characterization of the function of the IFJ; reviewed in Brass et al., 2005) and implicated in a cognitive control network (Cole & Schneider, 2007). In recent years, the IFJ has generated increased interest due to its involvement in a surprising variety of

high-level cognitive functions, such as top-down visual attention (Baldauf & Desimone, 2014), working memory (Zanto et al., 2010) and the implementation of novel task instructions (Muhle-Karbe et al., 2017), thus firmly positioning it within the multiple-demand system of the brain (Assem et al., 2020; Duncan, 2010; Fedorenko et al., 2013).

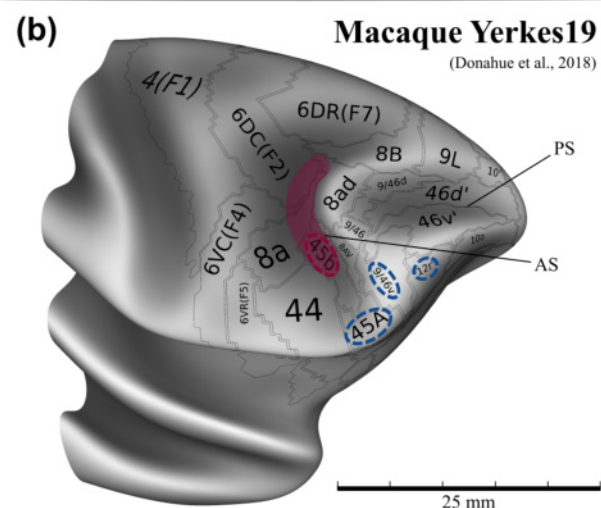
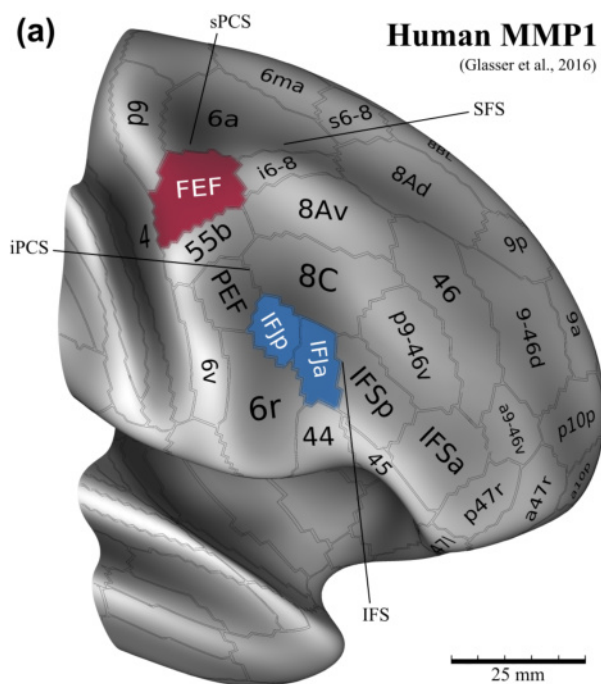


FIGURE 1 Putative homologies between the human and the macaque PFC displayed on the human MMP1 (a) and the macaque Yerkes19 atlases (b). The homologies between the human and the macaque PFC are, due to the lack of similar sulcal morphology (because the macaque brain has a single principal sulcus, in contrast to the human brain, which has two major sulci, the SFS and the IFS), best inferred based on structural and/or functional criteria, rather than morphological information. In the MMP1, the typical localization of the IFJ relative to the sulci likely corresponds to the IFJp (a) (see Section 2.2.2 for a detailed discussion). According to the study by Donahue et al. (2018), the human FEF would be the homologue of area 45b in the macaque (Schall et al., 1995), but it may also overlap with other brain regions (viz., 8a and 6DC(F2); see, e.g., fig. 1 in Schall, 2015). In the studies by Bichot et al. (2015, 2019), the authors identified a ventral prearcuate region (VPA) that was proposed as the human IFJ homologue and that overlapped with areas 46v, 45A and 12. Based on their injection sites, three regions that may correspond to the VPA were highlighted on the Yerkes19 atlas (b) (the regions 45A, 9/46v and 12r0

from the composite PFC parcellation by Donahue et al., 2018; PS, principal sulcus; AS, arcuate sulcus; both (a) and (b) were adapted from the datasets available in Balsa at <https://balsa.wustl.edu/>; Van Essen et al., 2017). At present, it is however unclear whether cytoarchitectonic maps in the macaque are appropriate for inferring homologies with the human PFC (see Section 2.2.1 for a discussion). In Section 2.5, we highlight some of the most intriguing proposals that aim at resolving these comparative neuroanatomical issues

2.2 | STRUCTURE

2.2.1 | Cytoarchitecture, chemoarchitecture and receptorarchitecture

Traditionally, cytoarchitecture has been the most prominent property used in defining cortical maps (Amunts & Zilles, 2015). However, with the advent of neuroimaging, the balance decisively shifted in favour of non-invasive in vivo methodologies (Eickhoff, Yeo, & Genon, 2018). In humans, the FEF and the IFJ were indeed initially defined and localized in stereotaxic space thanks to positron emission tomography (PET) and fMRI studies (Derrfuss et al., 2005; Paus, 1996; but see Foerster, 1931, and Penfield & Rasmussen, 1950, for earlier investigations based on electrical stimulation), and only subsequently their specific architectural properties were examined. However, establishing correspondences between cortical borders derived from architectural and functional information has proven challenging. Even if functional borders agree well with architectural ones (e.g., Brodmann areas [BAs]; Brodmann, 1909), some of the latter encompass many functional regions (and vice versa), so any straightforward extrapolation from one map to the other is likely insufficient (Amunts et al., 1999). Moreover, the undue reliance on comparative criteria to examine the architecture of these regions can also be misleading. For example, it could be very well the case that, especially in areas that followed a significant expansion in size in humans compared with other primates (Donahue et al., 2018), areas that underwent evolutionary change also present a different architecture and thus lie within incongruent BA.

These interpretative issues will become immediately apparent when describing the architecture of the FEF. In fact, a substantial impediment in the comparative study of the FEF was caused by the recognition that there are remarkable inconsistencies between the two most widely used cytoarchitectonic maps of the human and of the macaque (Brodmann, 1909; Walker, 1940), particularly in the PFC, in which borders were drawn relying on different cytoarchitectonic criteria, and no explicit comparative considerations were put forward during that process (Petrides et al., 2012). To resolve some of these discrepancies, Petrides and Pandya (1999, 2002) investigated the comparative cytoarchitecture of the dorsolateral PFC and the vlPFC and re-examined Brodmann's taxonomy in these brain districts. According to the neuroimaging evidence available at the time (in particular, the study by Courtney et al., 1998), the authors suggested that the human FEF is localized within BA8 and BA6, rather than in area 8Ad, in contrast to the macaque. Although the IFJ is not explicitly reported in their second study, we can speculate that this area corresponds to what the authors identify as BA6, BA44 and, to a lesser extent, area BA9/46v. Two subsequent studies have specifically investigated FEF as defined by fMRI evidence and then examined its cytoarchitecture and chemoarchitecture *ex vivo*. Rosano et al. (2003) investigated the

cytoarchitecture and chemoarchitecture of FEF in six subjects. They reported that several chemoarchitectonic features could segregate FEF from rostral regions in the middle frontal gyrus (MFG) and superior frontal gyrus. Their findings indicated that FEF is at a point of transition between the granular and agranular cortices in the vicinity of the superior PCS (sPCS). In a single case *ex vivo* study, Schmitt et al. (2005) found that cytoarchitecture differentiates two aspects of the putative FEF localized in an area of 2 mm parallel to the lateral convexity and an area of 8 mm in the depth of the PCS. This study also reported that, according to cytoarchitectonic criteria, FEF is for the most part localized in BA6.

On the other hand, the first characterization of the structure of the IFJ derives from a re-examination of a study by Amunts et al. (1999). In the resulting position paper, Amunts and von Cramon (2006) reported that a sharp change in cytoarchitecture and chemoarchitecture occurs in a region that corresponds to the functionally defined IFJ. The area analysed belongs to BA8, BA6 and BA44. In Amunts et al. (2010), the authors performed the post-mortem analysis of eight brains, which revealed that the receptor fingerprint of the left IFJ segregates this area from the ventral area 44d based on higher concentrations of AMPA, GABAA and M2 receptor densities (reviewed in Zilles & Amunts, 2018). Interestingly, the authors also reported the segregation of IFJ in two subregions along the banks of the PCS. This distinction parallels evidence from other methodologies (in particular, the studies by Glasser et al., 2016, and Zanto et al., 2010; the latter is discussed in Section 2.3.3), suggesting the presence of a robust subdivision within the IFJ. Therefore, it would be interesting to assess the agreement between architectural and functional criteria in segregating the IFJ (both from other brain regions and internally) and investigate whether neural populations with different selectivity and function could underlie this subdivision. In conclusion, based on the available evidence, we can tentatively describe FEF as a region characterized by a dysgranular architecture (i.e., with a weakly developed fourth layer), part of BA6 (and perhaps to a lesser extent, of BA8), and IFJ as a dysgranular region lying in the posterior bank of the IFS, in BA6, BA8 and BA44. However, due to the very limited sample available in post-mortem studies, the question that is crucially left open is whether these results can be generalized to the localization (and the borders) of FEF and IFJ as defined by non-invasive methods (primarily fMRI) in larger cohorts. Conversely, it is left open whether evidence derived from probabilistic structural atlases (e.g., Amunts et al., 2020) can be used to independently validate the localization inferred from fMRI experiments.

2.2.2 | Localization and relation to sulcal morphology

Traditionally, the FEF and the IFJ have been both localized along the banks of the sPCS and the inferior PCS (iPCS), the former in the vicinity of its intersection with the superior frontal sulcus (SFS), and the latter ventrally, in the vicinity of its intersection with the IFS (see Figure 1a). Due to the absence of compatible sulcal landmarks in monkeys (Donahue et al., 2018), the detailed comparative assessment of similarities in the organization of FEF and IFJ has proven very challenging (but see Neubert et al., 2014; Sallet et al., 2013). It also remains to be elucidated how inter-individual differences in the sulcal morphology affect the exact localization of FEF and IFJ. Of primary interest in this section are therefore

instances of spatial shifts and potential inversions between the respective locations of FEF and IFJ, which would lead to incomplete spatial segregation between these regions when their activity (as measured by fMRI) is pooled at the group level.

The correspondence between the macaque and the human FEF has been a puzzling aspect of FEF localization and function. In the study by Koyama et al. (2004), the authors compared the localization of the macaque and the human FEF to resolve discrepancies in FEF localization, which potentially stemmed from idiosyncratic methodological approaches in the two species. They measured fMRI blood oxygen level dependent (BOLD) activity in both species while performing visually guided saccades in blocked and event-related designs. They found that the execution of saccadic movements consistently activated similar regions in frontal and parietal cortices. The macaque dorsal lateral intraparietal region corresponded to the human superior parietal lobule (SPL), and the macaque FEF corresponded to the putative human FEF, localized at the intersection of SFS and PCS (BA6). Because activation peaks were also found in premotor regions in macaques (BA6), the authors concluded that the FEF presents a similar anatomical organization across the two species. In the study by Amiez et al. (2006), the authors' goal was to dissociate activity related to manual and saccadic responses, which according to previous neuroimaging evidence often overlapped nearby the junction of the SFS and the PCS. They analysed conditional hand responses and saccadic movements in a blocked-design fMRI experiment on a subject-by-subject basis to clarify the respective activation foci. Their study shows that three main variants can represent the morphology of the junction of the SFS and the PCS and that in all the subjects analysed, the activations associated with the execution of conditional hand movements and saccades tapped into a dorsal and a ventral portion of PCS junction with the SFS, respectively, agreeing with the available comparative evidence in non-human primates.

Concerning the exact localization of IFJ and its relation to sulcal morphology, the study by Derrfuss et al. (2009) reported that in 13 out of 14 of their participants, the activations found in a task-switching fMRI study were localized in the iPCS, nearby the junction with the IFS in the left hemisphere. Thus, similarly to the FEF, the localization of the IFJ appears to be tightly associated with the individual sulcal morphology and stable across subjects. Finally, in a study of outstanding interest to the scope of this work by Derrfuss et al. (2012), the authors reported an anatomical and functional double dissociation between the activations elicited by saccades versus button presses in the motor paradigm (in the inferior FEF [iFEF]) and incongruent versus congruent trials in the Stroop paradigm in the IFJ along the banks of the PCS. Of critical importance, the authors performed the analysis of activations at the subject level in the left hemisphere to localize both regions of interest (ROIs). In the case of the iFEF, the contrast between saccades and button presses was aimed at removing two major confounds: (1) this contrast allowed to keep sensory (i.e., auditory) stimulation balanced and to isolate activity specifically related to saccade execution; (2) saccades were executed in darkness to remove any change in visual stimulation during the task. The authors showed that for 16 of the 17 participants, these tasks (viz., the motor and the Stroop task) were successfully able to dissociate activations in the iFEF and the IFJ. Unfortunately, however, the lack of eye-tracking data is a limitation of this study. For

example, previous studies showed that imbalances in blinking behaviour in the absence of visual stimulation can contaminate BOLD signal and significantly alter activity in prefrontal oculomotor sites, such as FEF and the supplementary eye field (Bristow et al., 2005; Hupé et al., 2012). Thus, an alternative interpretation that eye blinks drove iFEF responses cannot be completely ruled out (Kato & Miyauchi, 2003; see also Amiez & Petrides, 2009, for a similar interpretation of iFEF activations).

In summary, sulcal morphology is a fundamental aspect of FEF and IFJ localization and underlies the spatial segregation between these regions. Future studies should investigate the development of the cortical folding in the plPFC and consolidate the brain mapping approaches that allow the dissociation of the activations found along the superior and inferior banks of the PCS.

2.3 | FUNCTION

In this section, we turn to describe and compare FEF and IFJ involvement in orchestrating functions and top-down control, such as visual attention, working memory and executive functions. There are undoubtedly many other aspects that differentiate the role of these areas in cognition. Still, we claim that it is precisely in their differential roles of top-down guidance that we find the most systematic and prominent differences between these two areas. This work is strongly influenced and inspired by the legacy and pioneering work by Patricia S. Goldman-Rakic, who carefully studied the organization and the functional specialization of the PFC (Goldman-Rakic, 1996; Wilson et al., 1993). In the following, we will focus on reviewing more recent human neuroimaging studies of FEF and IFJ activity, mostly in the form of fMRI and MEG, or combinations of the two methods. We choose this focus because the excellent spatial and temporal resolution of these (combined) tools allows measuring and modelling task-related activities in FEF and IFJ at an unprecedented level of detail, revealing important differences in their involvement in attentional and working memory tasks. Thus, all the remaining comparisons based on different cognitive subdomains and sources of evidence (e.g., lesion studies) are outside the scope of the present work.

To ease the exposition, this section will be organized around the discussion of six well-known functional dichotomies: modal versus supra-modal coding, presence versus lack of topographic organization, top-down versus bottom-up spatial attention, spatial versus non-spatial attention, spatial versus object-based working memory and position within versus outside the multiple-demand system. Although we acknowledge that some of these dichotomies have been in part superseded (e.g., top-down vs. bottom-up attention; Awh et al., 2012; Macaluso & Doricchi, 2013), we will attempt to discuss the evidence on a continuum, thus avoiding unilateral considerations on the role of FEF and IFJ in these dichotomies, and refer to novel theoretical frameworks whenever appropriate. The decision to structure this section in this specific way is essentially motivated by the basic understanding of attention and working memory as fundamental orchestrating functions, which provide the building blocks of other high-level cognitive functions, such as response inhibition, task-switching and more generally the hierarchical control of behaviour (Desimone & Duncan, 1995; Fuster,

2001; Goldman-Rakic, 1996). In accordance with this assumption, the dichotomies discussed also follow a gradual and ordered progression from sensory functions towards more abstract ones (i.e., detached from sensory input). Finally, we would also like to emphasize that the goal of the present review is primarily to facilitate the integration of the role of FEF and IFJ into already existing computational and neural frameworks of attention, working memory and cognitive control (Carrasco, 2011; Desimone & Duncan, 1995; Duncan, 2001; Itti & Koch, 2001; Miller & Cohen, 2001; Serences, 2016; Sreenivasan et al., 2014) by focusing on the implementation of the mechanisms posited by these models at the brain network level (Cole et al., 2013; Corbetta & Shulman, 2002; Fecteau & Munoz, 2006; Fiebelkorn & Kastner, 2020; Koechlin et al., 2003; Nee & D'Esposito, 2016; O'Reilly, 2010).

2.3.1 | Sensory domains (modal vs. supra-modal coding) and topographic organization

Prominent cognitive models posit that the brain areas involved in the selection of competing stimuli and responses need to be supra-modal in nature (Dux et al., 2006; Norman & Shallice, 1986; Pashler, 1994). However, recent studies using MVPA show that in the plPFC, several areas involved in these processes exhibit selectivity for specific sensory modalities (Michalka et al., 2015; Schwedhelm et al., 2020; Tamber-Rosenau et al., 2013). In Michalka et al. (2015), the authors used fMRI to investigate the hypothesis that the lateral frontal cortex is organized according to the selectivity to sensory modality by contrasting the activity elicited by a sustained covert visual attention task and an auditory task. In the majority of participants, the contrasts revealed activation foci localized in the sPCS and the iPCS, respectively. There was also a significant gap between the foci in the transverse gyrus of the PCS, where all subjects showed auditory selectivity. Interestingly, there was an additional auditory-biased region on the caudal portion of the IFS. This study also analysed the intrinsic (i.e., resting-state) functional connectivity of the previously defined regions with posterior visual and auditory areas. They showed that sPCS and iPCS activity positively correlated with visual attention areas and that activity in the transverse gyrus of the PCS and the caudal IFS correlated with auditory attention areas, whereas the reverse correlation was not found significant or was negative, thus showing the independence of these networks (this original finding was replicated in a larger sample in Tobyne et al., 2017). Finally, in a recent study employing a rule-based attentional selection paradigm, Germann and Petrides (2020) reported that in the left hemisphere, the ventral part of area 8A is involved in the selection of visual stimuli, whereas in the right hemisphere, its dorsal part is involved in the selection of auditory stimuli, which further supports the idea of sensory selectivity in the plPFC.

In parallel to the previous research line on sensory selectivity in the PFC, studies on the retinotopic organization across the cortex revealed that several foci in the frontal, parietal and occipital cortices show responses to visual stimulation that are organized in a topographic fashion (Benson et al., 2018; Sereno et al., 1995; Wang et al., 2015). These responses are modulated by attention (Saygin & Sereno, 2008) and are hypothesized subserving spatial attention and spatial working memory (Hagler & Sereno, 2006; Jerde et al., 2012; Kastner et al., 2007). In their seminal fMRI study, Mackey et al. (2017) developed a method to reliably elicit activations in frontoparietal regions and computed their population receptive fields

(Dumoulin & Wandell, 2008) using a model that accounts for non-linear responses to stimuli of varying size. In each of the five subjects analysed, the authors identified two topographic maps in the sPCS and the iPCS. Both these cortical patches contained a representation of polar angle and eccentricity. In the sPCS, the foveal representation was localized at the junction of the PCS with the SFS, which allowed the separation of this region in two visual field maps (referred to as sPCS1 and sPCS2 below) containing a complete representation of contralateral space. In contrast, the organization of the iPCS was less clear, but this area seemed to be still capable of representing eccentricity and the contralateral space in a systematic way. The authors related these newly defined maps to the topographic atlas by Wang et al. (2015) and the multimodal parcellation 1.0 (MMP1) by Glasser et al. (2016). The sPCS2 corresponded to the FEF in both of those atlases, whereas the sPCS1 corresponded in large parts to the more dorsomedial areas 6a and 6d in the MMP1. The iPCS corresponded to the ventrolateral premotor eye field and the posterior IFJ (IFJp) regions, and area 6r in the MMP1, but this correspondence varied considerably across subjects and between hemispheres. Although the sample size of this study was quite small, and thus the topographic mapping technique that the authors developed requires to be validated in a larger sample, this study suggests that FEF can confidently be included in the set of topographic visual areas. The evidence for a topographic organization of IFJ is instead comparatively weaker. Indeed, if IFJ may to some extent represent eccentricity, its overlap with activations found in the iPCS was very loose. Furthermore, evidence in non-human primates indicates that neurons in the vlPFC (specifically, in the ventral pre-arcuate region, the putative homologue of the human IFJ; Bichot et al., 2015, 2019) have extensive receptive fields that can sometimes extend to the ipsilateral space—a fact that again suggests little evidence of topographic organization (Bichot et al., 2015, 2019).

In summary, although it has been recently suggested that FEF and IFJ are both primarily unimodal (visual) areas, we reviewed here novel evidence that favours a more general involvement of the FEF in spatial tasks, as only FEF contains a precise topographic representation of contralateral space, whereas the IFJ (and in particular, the IFJp as defined according to the MMP1) has only quite limited overlap with topographically organized areas (as the iPCS activations found by Michalka et al., 2015, and Tobyn et al., 2017; see also Mackey et al., 2017). Further work will be required to characterize the organization of topographic maps in the plPFC and their correspondence with the parcellation schemes derived from multimodal MRI data (Glasser et al., 2016; Neubert et al., 2014; Sallet et al., 2013).

2.3.2 | Top-down versus bottom-up spatial attention

Much of the early neuroimaging studies (PET and fMRI) on the brain regions and networks subserving visual attention was dedicated to understanding how the brain achieves top-down control over visual input or, conversely, how attention is automatically driven by bottom-up factors (Corbetta & Shulman, 2002). These pioneering studies coalesced in the seminal proposal that a dorsal attention network (DAN; with FEF and the intraparietal sulcus [IPS] as primary nodes) controls top-down visual selection. Although it is not explicitly

mentioned, also parts of the IFJ seem to be localized within this network, with MFG as the most closely labelled brain structure. In contrast, a right-lateralized ventral attention network (VAN), with inferior frontal gyrus (IFG) and the temporoparietal junction (TPJ) as primary nodes, was hypothesized to be involved in the automatic reorienting of attention to external (salient) stimulation (Corbetta & Shulman, 2002). Although this proposal was very elegant in the way it reconciled the neuroimaging evidence available at the time, and it was successfully able to isolate the main nodes of the attention networks that were involved in a variety of experimental tasks (reviewed in Fiebelkorn & Kastner, 2020), and also in spontaneous, resting-state activity (Fox et al., 2006), it suffered from several limitations. First of all, earlier studies failed to appreciate the distinction between reorienting to predictable versus unpredictable stimuli (Shulman et al., 2009), and secondly, between reorienting of attention and the evaluation of the appropriate stimulus-response mapping, mainly due to the lack of time resolution (Han & Marois, 2014). Finally, these initial studies were not designed to model directed interactions between DAN and VAN nodes. Vossel et al. (2012) addressed the latter question in an fMRI study by analysing the effective connectivity between FEF, IPS, and the right TPJ and IFG (likely also comprising the right IFJ) using dynamic causal modelling. In their spatial task, the participants were instructed to discriminate an orientation grating shown at the right or the left of the fixation, and the predictability of the spatial cue was manipulated between blocks (90% vs. 60%; the subjects were made aware of the manipulation by the colour of the cue). The author contrasted valid > baseline and invalid > valid trials to extract the DAN (FEF, IPS) and VAN (IFG, TPJ) nodes, respectively, at the single-subject level in a whole-brain analysis. They then separately evaluated a wide array of competing models of modulatory effects within the DAN and VAN nodes, and from/to the visual cortex, employing a random effect Bayesian model. This analysis revealed that, in the DAN, the model with the highest empirical support consisted of bilateral connections between FEF and IPS of both hemispheres, and between the right and left FEF. In the VAN, a model with bilateral connections from the visual cortex to the right TPJ and from there to the right IPS and IFG was best supported by the data. They also tested the effect of validity and cue predictivity in the modelled VAN connections and showed that in all areas, activity was increased in invalid, high cue predictivity trials. Moreover, the connection between right TPJ and right IPS was enhanced in this condition, indicating a potential communication mechanism between the VAN and DAN, suggesting that the VAN is right lateralized.

Within a similar theoretical framework, the fMRI study by Wen et al. (2012) tested the interactions between the DAN and VAN in a spatial attention task using Granger causality, and the functional role of these two networks for behaviour. Their task consisted of a spatial cue followed by a 2.5-s delay, after which the subjects were required to respond to an unlikely target (20% of the trials) in the valid condition and to ignore the stimulus in the unattended hemifield. The authors first contrasted attention blocks with passive-view blocks to isolate the main DAN and VAN nodes, which comprised the bilateral FEF and IPS, and the right anterior MFG, the right posterior MFG and the right TPJ (and also additionally, the bilateral dorsal anterior cingulate cortex and anterior insula), respectively. After computing Granger causality between all ROI pairs, they sorted their behavioural results (reaction time [RT] and accuracy) in bins and correlated the binned values with the Granger-causal values.

The results suggest that Granger-causal influences from the rIPS to the rTPJ are associated with increased accuracy, whereas the reverse influences from rTPJ to rIPS are detrimental to behavioural performance (both in RT and in accuracy). Moreover, by aggregating data from all the DAN and VAN ROIs, the authors showed that Granger-causal influences from the DAN to the VAN were again associated with increased accuracy, whereas influences from the VAN to the DAN led to worse RT, which further supported the results from the single ROI analyses. Interestingly, however, they also noted that the right posterior MFG (which seems to match quite well the location of the IFJ according to the sulcal landmarks) had a more ambiguous relationship with the DAN because it had directional influences on the rFEF, lIPS and rTPJ, all of which correlated positively with enhanced performance. Overall, the authors interpreted these findings as consistent with a model in which the DAN exerts top-down control and suppresses VAN activity to achieve efficient filtering of distracting stimuli, whereas the VAN is mainly involved in breaking the attentional set.

As the role of the FEF in top-down attention was already well established by both comparative and fMRI evidence (Buschman & Miller, 2007, 2009; Corbetta, 1998; Corbetta & Shulman, 2002; Gregoriou et al., 2009; Kastner & Ungerleider, 2001; Moore & Armstrong, 2003), one of the aims of the following research was to understand the contributions of the IFJ to the DAN and VAN. Asplund et al. (2010) investigated the effects of the interaction between goal-driven and stimulus-driven factors on fMRI activity during the performance of a non-spatial (i.e., centrally presented) rapid serial visual presentation task (RSVP). Unbeknownst to the participants, they inserted a human face in a small percentage of trials that acted as an irrelevant salient stimulus and caused a marked decrease in target detection (they refer to this effect as surprise-induced blindness). Their results show that, in the first two presentations of the distractor, there was an increase in activity in the IFJ and TPJ, after which neural responses adapted to the distractor, and that this modulation matched the behavioural performance in surprise trials. The authors also found evidence of increased activation in the FEF and IPS, although at longer delays (3 s), which therefore was not affecting behavioural performance. Thus, their study suggests the idea that the IFJ may act as an interface between the stimulus-driven VAN and the goal-driven DAN and that it could mediate the conscious perception of behaviourally relevant stimuli. Han and Marois (2014) attempted to dissociate the activity related to transient reorienting from sustained activity related to the evaluation of the stimulus in an Rapid Serial Visual Presentation (RSVP) task contrasting short versus long (1 and 10 s) ‘oddball’ trials. The results of their experiments (fMRI exp. 1–2) revealed that the TPJ and IFJ showed both transient and sustained responses to salient stimuli, whereas several other areas in the PFC (e.g., the insula and the cingulate cortex) had transient responses only, a result that implicates these regions in ongoing evaluative processes. Finally, in their fMRI study, Tamber-Rosenau et al. (2018) investigated how the DAN and VAN contribute to transient and sustained attentional processes. They used an endogenous spatial cueing paradigm with variable delays in target presentation to specifically tease apart the role of the IFJ in the configuration and maintenance of attentional priority. They found that in the right hemisphere, the FEF and IPS showed evidence of both transient (i.e., at the end of the cue and the target presentation) and sustained activities (i.e., during the whole delay period). In contrast, the bilateral IFJ showed only evidence of

transient activity, pointing to an initial involvement of this region in the configuration of the attentional state. We note that a potential reason for the discrepancy with the results reported by Han and Marois (2014) is that in the latter study, the authors focused on analysing only longer delay trials (9, 13 and 15 s) as their original goal was to dissociate the IFJ from DAN nodes (i.e., the FEF and IPS), and therefore, they defined sustained activity as one that is significantly elevated relative to baseline during the entire delay period. Accordingly, although the right IFJ showed evidence of sustained activity if delay periods were pooled together, this was no longer the case when the results were further analysed separately for each delay period. Concerning the DAN nodes, their results are consistent with models of a priority map within the FEF (similar to priority maps in the posterior parietal cortex; see Fecteau & Munoz, 2006; Itti & Koch, 2001; Thompson & Bichot, 2005; Zelinsky & Bisley, 2015). The function of the frontal priority map is to integrate bottom-up and top-down signals and to guide perceptual and action selection (Fecteau & Munoz, 2006).

However, there are still aspects of the role of the FEF and IFJ in top-down selection that remain quite elusive. In macaques, the latency of FEF responses has been estimated to be approximately 40 ms, with some neurons exhibiting latencies comparable with V1 and V2 neurons (Bullier, 2001). In a recent electrocorticographic study, Martin et al. (2019) found comparable latencies in the human FEF in response to a spatial cue (62 ± 5 ms), which were again in the order of early visual cortex latencies. However, surprisingly, they reported that the effects of attentional modulation were more pronounced, and their latencies were shorter, in extrastriate areas and the parietal cortex, compared with frontal and visual cortices. These results highlight the need of pursuing similar research efforts to successfully bridge electrophysiological research in non-human primates and humans. To summarize, whereas the FEF is consistently involved in top-down spatial selection and may provide the instantiation of a priority map where top-down signals are integrated with bottom-up activity and maintained, the IFJ acts as a flexible hub that toggles between the DAN and VAN activities and modulates activity in the DAN according to the current behavioural demands and context.

Finally, although the in-depth discussion of this subject is partly outside the scope of the present work and would certainly deserve to be reviewed separately, here, we would like to describe and point the reader to outstanding transcranial magnetic stimulation (TMS) evidence that helps to reveal the contribution of the FEF and IFJ to attentional control and working memory processes, thus complementing the correlational studies described earlier with causal evidence. In Ruff et al. (2006), the authors combined fMRI with concurrent TMS and revealed that repetitive TMS over the right FEF increases the BOLD signal in peripheral locations and reduces it in a central location in retinotopic regions (V1–V4) depending on the TMS intensity in an additive way, both in the presence and absence of visual stimulation. This effect was shown to be behaviourally relevant by a follow-up psychophysical experiment, in which TMS over the same site (rFEF) enhanced the perceived contrast of a peripheral Gabor patch in both visual hemifields. Subsequent studies were able to replicate and extend this set of findings to a variety of visual tasks (see, e.g., Bardi et al., 2012; Neggers et al., 2007; Ronconi et al., 2014; Taylor et al., 2007; Vernet et al., 2014, for a

review). In their innovative multimodal study, Marshall et al. (2015) further uncovered the neural mechanisms that underlie FEF influences over occipital sites. They first localized FEF sites at the individual subject level in a preliminary fMRI session. They subsequently administered continuous theta burst stimulation (cTBS) with TMS to the left and right FEF, and a third control site (vertex), and recorded the neural activity in the 30 min afterward using MEG while the participants were performing a spatial attention task. Their results show that cTBS over the rFEF (co-registered to the T1-w image) impaired performance for contralateral stimuli, decreased anticipatory alpha power modulation in the contralateral hemisphere and increased gamma power in the left hemisphere after rFEF stimulation. Together, these findings highlight the oscillatory signatures of the top-down control exerted by the FEF over the occipitoparietal cortex and potentially suggest a role for interhemispheric interactions. The role of the FEF in top-down control was further supported by a recently published study by Veniero et al. (2021), which combined online TMS with electroencephalography (EEG). In their first experiment, the authors applied single-pulse TMS to the rFEF and showed that this pulse led to an oscillatory alignment in the beta frequency band as measured from occipital channels. In a second experiment, they applied single-pulse TMS to the rFEF while the participants were performing a motion discrimination task. They showed once again that this pulse led to an oscillatory alignment and, more importantly, that this modulation caused an analogous cyclic effect on visual performance in the same beta band. In two follow-up experiments, these effects on visual perception were confirmed via dual-site TMS on the rFEF, on the one hand, and on rV5/rV1, on the other, by examining phosphene perception. This analysis revealed a similar rhythmic modulation as in the previous experiments of rV5 excitability, but not rV1, thus providing anatomical specificity to the results of their study.

The TMS evidence on the IFJ is much scarier, but nevertheless essential to understand its role in top-down control. The influential study by Zanto et al. (2011) used a non-spatial, feature-based task where subjects were asked to either remember colour information and ignore motion direction or vice versa, and respond to a probe item (see Zanto et al., 2010, for more details on the methodology; described in the following section). They applied repetitive 1-Hz TMS on the right IFJ (defined in a separate fMRI experiment) for 10 min and measured EEG while the participants were performing their behavioural task. They showed that in the first half of the experiment, repetitive TMS decreased behavioural accuracy and the amplitude of the P1 component in the ‘attend colour’ condition. These results were further confirmed by analysing the phase coherence between frontal and posterior electrodes in the alpha band, which was previously identified as a signature of neural modulation, and that decreased following repetitive TMS. In the study by Muhle-Karbe et al. (2014), the authors investigated the role of the left IFJ and left IPS in task preparation. These nodes were defined by performing an fMRI meta-analysis of task-switching studies (45 studies) using the activation likelihood estimation (ALE) technique (Eickhoff et al., 2012) and targeted them by repetitive TMS during the execution of a cued task-switching paradigm. This paradigm contained blocks in which the task goal was repeated, but subjects had to change their response set, and blocks in which the response set was constant, but they had to reconfigure their task goal. Crucially, by delivering repetitive

TMS on these sites before the target onset, the authors revealed a double dissociation between the IIFJ and IIPS in task preparation; namely, that the stimulation of the former impaired the reconfiguration of task goals, but not of the response set, and conversely, that the stimulation of the latter impaired the updating of the response set, but not of the task goal. Finally, in a third experiment, the authors showed that the IIPS was also implicated in reconfiguring the task goal, but at a later stage in the information processing cascade. These results therefore highlight the IIFJ as one of the sources of the top-down signals to posterior parietal areas that it is crucial to cognitive control functions (for converging evidence, see Hippmann et al., 2019; Muhle-Karbe et al., 2018; Verbruggen et al., 2010). In addition, as in both the study by Zanto et al. (2011) and Muhle-Karbe et al. (2014), the task-relevant dimension was feature based (colour/motion and shape/colour, respectively), this suggests the intriguing possibility that the IFJ may be specifically involved in encoding and manipulating information in a non-spatial (feature- and object-based) representational format. We will elaborate more in detail on this suggestion in the general discussion, where we will also provide a concrete example of how TMS could be used to directly address this open question. Thus, now we will move on to discuss more broadly the relationship of the FEF and IFJ to spatial and non-spatial selective mechanisms.

2.3.3 | Spatial versus non-spatial attention and spatial versus object working memory

Functionally, it is very well possible to dissociate the behavioural effects and the neural mechanisms of spatial versus feature- and object-based (i.e., non-spatial) attention (Carrasco, 2011; Desimone & Duncan, 1995; examples of the classic spatial and non-spatial cueing paradigms are shown in Figure 2). Indeed, whereas spatial attention enhances the neural activity that codes the location of the attended stimulus (Kastner & Ungerleider, 2001), non-spatial attention acts globally on the entire visual scene (Baldauf & Desimone, 2014; Serences & Boynton, 2007; Störmer & Alvarez, 2014) and boosts the signals that code for the attended feature or object (i.e., through the ‘attentional template’; Desimone & Duncan, 1995), while also suppressing irrelevant, distracting information (Gaspelin & Luck, 2018). As we have seen, in the pLPFC, some areas adjacent to and including the FEF possess a topographic organization (reviewed in Section 2.3.1), thus being well adept to provide top-down location-specific modulation of neural activity. In contrast, another set of areas have extensive receptive fields (Bichot et al., 2015, 2019), which often encompass also the ipsilateral hemifield, which may account for the global nature of their modulation on visual processing. Because the attentional template needs to be held active during the task, it has been proposed that sustained, top-down attention (both spatial and non-spatial) relies on the same neural machinery as working memory processes, both in terms of their cognitive routines and the brain networks involved (Chun et al., 2011; Gazzaley & Nobre, 2012; Zelinsky & Bisley, 2015). It is widely agreed that perceptual attention and working memory are intimately linked (Awh & Jonides, 2001; Baddeley, 1993; Olivers, 2008). Not only is it a crucial component of top-down perceptual attention to keep templates for targets of the perceptual selection internally sustained over time (e.g., Awh et al., 1998; Chun et al., 2011; LaRocque et al., 2013; Oberauer, 2019). In this sense, Kiyonaga and Egner (2013) described the two components in an integrative account as internal versus external selection processes,

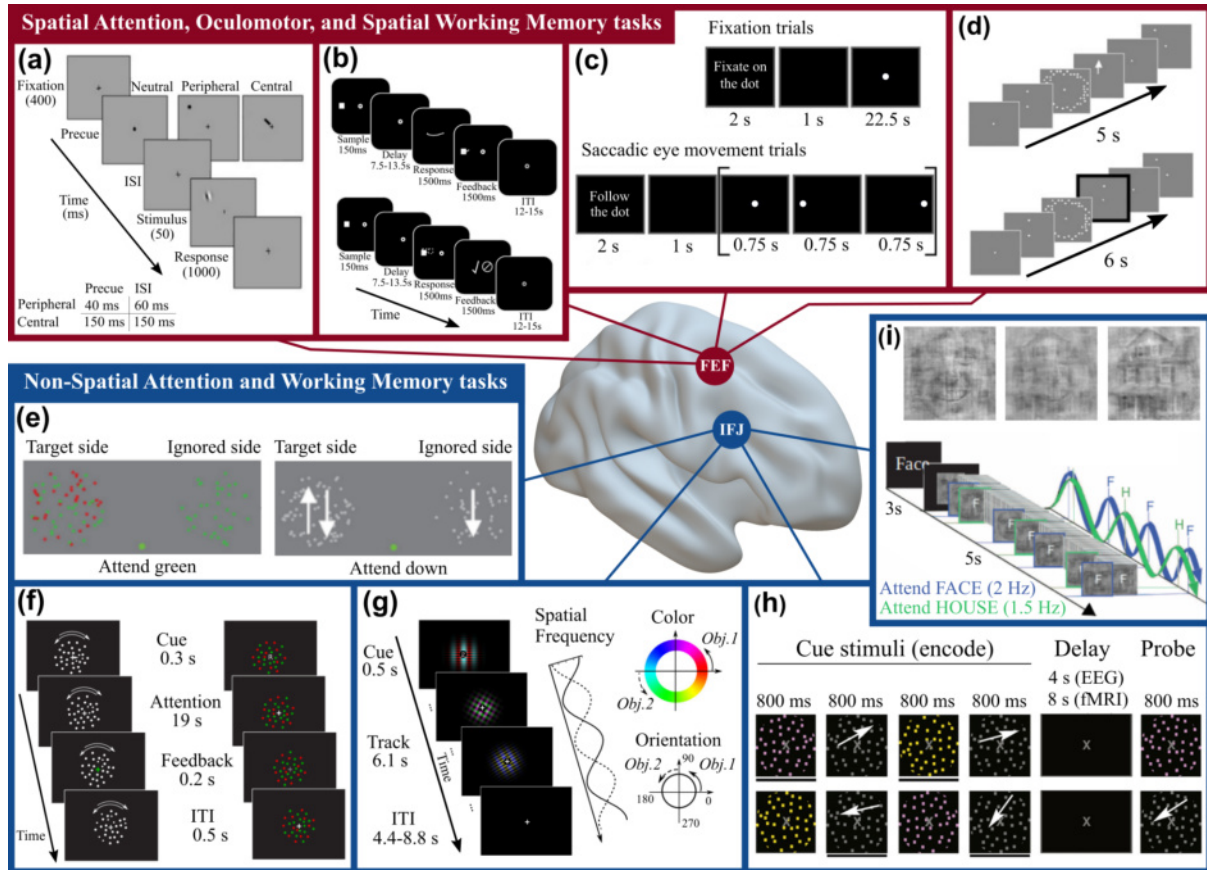


FIGURE 2 Paradigms that allow disentangling spatial and non-spatial attentional and working memory mechanisms. Red outline: Paradigms that involve a strong spatial component. The fundamental basis of all the tasks shown in this group is represented by the spatial cueing paradigm (a) (adapted from Carrasco, 2011). (b) The tasks from the study by Srimal and Curtis (2008), consisting of a memory-guided saccade (top) and a spatial item recognition task (bottom). (c) The saccadic eye-movement paradigm from the study by Amiez et al. (2006; adapted from Amiez & Petrides, 2009). Top row: Control task, in which subjects keep fixation. Bottom row: Experimental task, in which subjects need to perform a sequence of visually guided saccades. This paradigm represents the classical FEF fMRI localizer. (d) The memory-guided saccade task from the study by Kastner et al. (2007). This study provided compelling evidence of the presence of topographic maps in the PFC (and crucially, in the sPCS/SFS, encompassing the FEF). Blue outline: Paradigms that involve purely non-spatial mechanisms. (e and f) The feature-based attention tasks from the studies by Zhang et al. (2018) and Liu et al. (2011). In these tasks, the subjects are asked to hold fixation and are instructed by an endogenous cue to pay attention to the features of a stimulus (either colour or motion) and to detect a sudden change in luminance of a dot or an increase in its speed of motion. Because this imperative event can happen randomly in each portion of the cloud-like stimuli, spatial information is rendered ineffective for solving the task at hand (in the study by Zhang and colleagues, half of the dots were replaced and reappeared at new locations each 100 ms to discourage even more the use of spatial strategies; the attended and ignored sides were blocked). (g) The purely object-based attention task devised by Liu (2016). The colour, orientation and spatial frequency of the two superimposed Gabor patches

changed simultaneously over the trial, so the subjects needed to pay attention to their identity to effectively perform the task. (h and i) The working memory task used by Zanto et al. (2010) and the object-based attention task from the study by Baldauf and Desimone (2014). All these feature- and object-based attention and WM tasks engage the IFJ, which is responsible for modulating activity in downstream visual areas (e.g., MT+, V4, PPA and FFA) to enhance behavioural performance (Baldauf & Desimone, 2014; Zhang et al., 2018)

respectively. Experimentally, also many forms of interactions have been described between working memory and attention (Olivers, 2008). For example, Kim et al. (2005) showed that increased ongoing working memory load reduces perceptual Functionally, it is very well possible to dissociate the behavioural effects and the neural mechanisms of spatial versus feature- and object-based (i.e., non-spatial) attention (Carrasco, 2011; Desimone & Duncan, 1995; examples of the classic spatial and non-spatial cueing paradigms are shown in Figure 2). Indeed, whereas spatial attention enhances the neural activity that codes the location of the attended stimulus (Kastner & Ungerleider, 2001), non-spatial attention acts globally on the entire visual scene (Baldauf & Desimone, 2014; Serences & Boynton, 2007; Störmer & Alvarez, 2014) and boosts the signals that code for the attended feature or object (i.e., through the ‘attentional template’; Desimone & Duncan, 1995), while also suppressing irrelevant, distracting information (Gaspelin & Luck, 2018). As we have seen, in the plPFC, some areas adjacent to and including the FEF possess a topographic organization (reviewed in Section 2.3.1), thus being well adept to provide top-down location-specific modulation of neural activity. In contrast, another set of areas have extensive receptive fields (Bichot et al., 2015, 2019), which often encompass also the ipsilateral hemifield, which may account for the global nature of their modulation on visual processing. Because the attentional template needs to be held active during the task, it has been proposed that sustained, top-down attention (both spatial and non-spatial) relies on the same neural machinery as working memory processes, both in terms of their cognitive routines and the brain networks involved (Chun et al., 2011; Gazzaley & Nobre, 2012; Zelinsky & Bisley, 2015). It is widely agreed that perceptual attention and working memory are intimately linked (Awh & Jonides, 2001; Baddeley, 1993; Olivers, 2008). Not only is it a crucial component of top-down perceptual attention to keep templates for targets of the perceptual selection internally sustained over time (e.g., Awh et al., 1998; Chun et al., 2011; LaRocque et al., 2013; Oberauer, 2019). In this sense, Kiyonaga and Egner (2013) described the two components in an integrative account as internal versus external selection processes, respectively. Experimentally, also many forms of interactions have been described between working memory and attention (Olivers, 2008). For example, Kim et al. (2005) showed that increased ongoing working memory load reduces perceptual distraction. Similarly, eye movements systematically interfere not only with attention but also with working memory (Lawrence et al., 2004). Further, Lepsien et al. (2011) showed that voluntary attention shifts modulate the maintenance of working memory. Finally, Mendoza-Halliday and Martinez-Trujillo (2017) demonstrated that in the lateral PFC of the macaque, identical neuronal populations encode both perceived and memorized visual features. Generally, when discussing attention control, it is worth emphasizing that an attentional cue can be given with or without stimuli present in the environment (see, e.g., Figure 2a–c,e–h): if there are stimuli in the environment directly following the cue (e.g.,

moving dots), it is more complicated to determine experimentally to which extent the neural activity in the cue-target interval reflects top-down control signals as opposed to being evoked by sensory input itself. In this section, we therefore build upon the hypothesis that both attention and working memory functions are underlaid by overlapping prefrontal activity. We will thus review in a unitary framework the evidence on how spatial and non-spatial processes are mediated by the FEF and the IFJ, respectively.

Inspired by studies on non-human primates and the pioneering work of Goldman-Rakic and colleagues (Goldman-Rakic, 1996; Scalaidhe et al., 1997, 1999; Wilson et al., 1993), researchers originally investigated the segregation of spatial and object working memory circuits in the human plPFC, but the evidence in support of this claim was mixed (Rao et al., 1997; Wager & Smith, 2003, for a landmark meta-analysis of early neuroimaging studies). Courtney et al. (1998) showed that a distinct cluster in the SFS (localized anteriorly to the FEF) was predominantly involved in spatial working memory, rather than working memory for object classes, such as faces. However, their interpretation was challenged by Owen et al. (1998). They hypothesized that the difference in the involvement of dorsal and ventral prefrontal regions was not due to the information content being encoded by these regions (i.e., location vs. object information) but rather the result of dissociation in other underlying cognitive processes. In particular, in their study, they showed that, when monitoring requirements were precisely matched between the spatial working memory and the non-spatial working memory task, both tasks elicited overlapping activations in the mid-dorsolateral PFC (BA46 and BA9/46). Despite these contrasting results, the dispute was far from settled and was from then on centred around how the plPFC acts as a gateway to establish priority on sensory inputs to implement goal-driven behaviour, and the nature of its selectivity to sensory information as opposed to the types of cognitive processes, the task's executive demands or practice with it (Constantinidis & Qi, 2018; O'Reilly, 2010; Wager & Smith, 2003). More recently, thanks to the improvements in fMRI data acquisition, and the availability of more sophisticated analytic tools (MVPA, and meta-analytic modelling techniques), the hypothesis of dorsoventral segregation based on the selectivity of plPFC neurons for spatial versus non-spatial informational content regained considerable interest in the field (see, e.g., the meta-analysis by Rottschy et al., 2012, for the dissociation of working memory activation foci related to object identity and location in the plPFC).

The initial neuroimaging evidence on the spatial selectivity in the FEF was strongly tied to studies investigating the overlapping mechanisms of covert and overt (i.e., via eye movements) visual selection (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995; Moore & Armstrong, 2003; Posner, 1980). Influenced by the premotor theory of attention (Rizzolatti et al., 1987), these studies predicted that the same brain regions involved in the planning and the execution of saccadic eye movements should also mediate covert shifts of attention (Corbetta, 1998). Several independent groups found that covert and overt spatial attention tasks consistently activated overlapping networks that included the FEF. This lent indirect support to the hypothesis of a premotor origin of covert spatial attention signals (Corbetta et al., 1998; Fiebelkorn & Kastner, 2020; Moore & Fallah, 2001; but see Thompson et al., 1997; for evidence of a link between microsaccades and covert

attention, see Lowet et al., 2018). Although following research has to some extent challenged this view, for example, highlighting that in the FEF not all neurons have visuomotor and motor functions (Schall, 2015), implying that covert and overt signals might originate from different neural populations, these studies were pivotal in establishing the FEF as a core region for spatial attention. The idea of spatial selectivity in FEF neural populations was further strengthened by the observation of topographically organized maps in this region (reviewed in Section 2.3.1), which encoded the attended location in a priority map via sustained activity during the delay period of attention and working memory paradigms (Awh & Jonides, 2001). Consistent with this view, a groundbreaking study by Jerde et al. (2012) showed that in the sPCS (likely, within the FEF) and IPS2, decoding techniques could cross-predict BOLD activity in the spatial tasks the subjects were performing (i.e., covert attention, working memory or overt saccadic motor task; Figure 2c). Their MVPA classifier was separately trained on each task's data and predicted activation patterns in the two left-out tasks, again showing that the networks involved in these functions share a significant degree of overlap in the close vicinity of the FEF. Even more strikingly, this activity was shown to be tied to the stimulus location (because the ROIs were extracted using retinotopic mapping), thus providing a very elegant demonstration that these areas are primarily involved in visuospatial selection, and agnostic to the behavioural response required (as one would assume if the FEF and IPS worked as spatial priority maps). One critical aspect in understanding the organization of the FEF is whether the tightly coupled functions of spatial attention, oculomotor control and spatial working memory are all implemented strictly inside the FEF, or involve also other adjacent brain areas, and whether they can be assigned to one or multiple subdivisions of the FEF. Previous studies were not able to exactly clarify the relationship between spatial attention and spatial working memory within the FEF, mostly owing to the fact that topographic mapping techniques have not been yet standardized for prefrontal regions and that previous studies often used hybrid (i.e., spatial and non-spatial) visual stimulation paradigms to elicit activations in the FEF (Hagler & Sereno, 2006; Mackey et al., 2017; Saygin & Sereno, 2008). In the rhesus macaque, the area involved in spatial working memory lies immediately anterior to the FEF (BA46; Funahashi et al., 1989; Fuster & Alexander, 1971), but the often incompatible arrangements of prefrontal areas and inconsistencies in BA labelling prevent a straightforward translation of this anatomical evidence from this species to humans (as previously discussed in Section 2.2.1). Kastner et al. (2007) employed four purely spatial tasks to examine the relationship between spatial working memory, spatial attention and oculomotor control in the FEF and to enable a more direct comparison with the typical working memory paradigms used in the non-human primate literature (Figure 2d). Their study showed considerable overlap between the activations in the memory-guided saccade task and the spatial working memory tasks in the sPCS/SFS (i.e., the FEF) and in the iPCS/IFS. The authors interpreted this finding proposing that the iPCS/IFS region should be considered the human homologue of the region specialized for spatial working memory in monkeys, which is not however fully consistent with other comparative evidence (Constantinidis & Qi, 2018). Nevertheless, this study was crucial in establishing the correspondence of spatial attention and working memory maps in the plPFC (see also Srimal & Curtis, 2008, for correspondences within the FEF; the tasks employed in the latter study are reported in Figure 2b).

Regarding the hypothesis of feature and object selectivity in the vIPFC, early neuroimaging studies on working memory (Owen et al., 1998; Wager & Smith, 2003) may have failed to observe evidence in favour of it for a simple and yet crucial experimental factor. When a stimulus is presented in the periphery, its features and identity likely need to be bound to its actual location in the visual field, but this process is a by-product of the spatial arrangement of the stimuli, and not universally valid for visual features that are not bound to a specific location in space (e.g., if they are presented holistically over the complete visual field). Although in everyday life visual features are often bound to specific locations in the periphery, a much more stringent way to measure pure feature- and object-based mechanisms is only achieved in experimental settings where no spatial information can be used to solve the task at hand. Several paradigms meet this fundamental requirement, the most common ones involving tasks in which the subjects are instructed to maintain fixation and to perform the visual detection/discrimination of a target appearing in several superimposed, spatially overlapping stimuli (Baldauf & Desimone, 2014; Carrasco, 2011; Serences et al., 2004).

Another potential methodological issue of previous studies was that spatial and non-spatial cues were often presented within the same experimental block (see, e.g., Giesbrecht et al., 2003), and this could have potentially biased the subjects' strategies (Slagter et al., 2007). In the study by Greenberg et al. (2010), the authors investigated whether voluntary shifts of attention towards a location or a feature (i.e., colour) engaged a common source in the attention networks. The participants were instructed to covertly attend one of four clouds of moving dots, one red and one green dot cloud overlapping in the left and right hemifield, respectively, and to either hold attention at the selected location and switch colour (when the dots in the clouds moved downwards) or hold colour and switch location (when the dots moved upwards). The results of their univariate analysis show that the bilateral mSPL, FEF/supplementary eye field and left MFG/IFG all showed transient responses to shifts of attention to both location and colour time locked to the cue. Interestingly, MVPA revealed above-chance accuracy in the mSPL for location and colour shifts, indicating that this region may host neural populations that are tuned to spatial and feature information. Although these results importantly suggest that several regions in the PFC may act in coordination to perform shifts of spatial and feature-based attention, they do not reveal the temporal structure and the interplay between those processes, as the experimental set-up used visual features in the periphery, mixing spatial and non-spatial selection processes. Liu et al. (2011), on the contrary, targeted purely feature-based attentional mechanisms in an fMRI study. The authors conducted two experiments in which the subjects were asked to attend to motion and colour information to detect random increases in dot motion velocity and luminance, respectively, on stimuli superimposed at the central fixation (Figure 2f). In their deconvolution univariate analysis, they identified four regions in which activity was sustained above baseline during both tasks: the aIPS, FEF, vPCS and the medial superior frontal gyrus. MVPA revealed that signals related to colour and motion could be classified above chance in all these ROIs, including the FEF. Thus, the authors interpreted these findings by proposing that PFC may represent attentional priority, regardless of the type of attended feature. Unfortunately, however, overt eye movement behaviour was not

controlled inside the scanner leaving the possibility that systematic eye movement patterns contributed to the signal decoded from the FEF.

Using similar stimuli with centrally presented dot clouds, Zanto et al. (2010) combined fMRI and EEG to investigate the top-down modulation of feature processing during working memory encoding. In their task, participants viewed four sequential frames of overlapping dots and had to remember either their colour or motion direction and ignore the opposite dimension to respond to a probe stimulus (Figure 2h). In the fMRI experiments, areas V4 and V5/hMT+ (selective for colour and motion information, respectively) were localized at the subject level using a one-back working memory task. Seed-based functional connectivity of these regions was then used to identify the regions that exhibited increased connectivity in the attend colour versus ignore motion (and vice versa) condition of the experiment. This analysis revealed that only the IFJ was involved in the modulation of both V4 and V5/hMT+ activities and that the putative sources of this modulation formed part of separate subregions in the former. EEG source localization was used to analyse the temporal profile of activity corresponding to the right IFJ and three posterior sites because V4 activity modulation correlated with increased V4-to-right IFJ functional connectivity. Phase-locking values between the rIFJ and central electrodes in the 70- to 200-ms window of interest in the alpha frequency band were significantly greater when recall performance was above the median in the colour task. This analysis of coherence suggests that the alpha band might reflect top-down modulation of colour processing. The authors also highlighted that the rIFJ subregion involved in motion processing is more dorsal, whereas the colour subregion is more ventral, thus providing evidence that the segregation of the visual streams extends up to the plPFC within the IFJ.

In the study by Sneve et al. (2013), evidence of the transient role of the IFJ was found during the performance of a working memory task requiring delayed orientation discrimination. In particular, this study found increased bilateral activity in the IFJ during the encoding process compared with a control task where no working memory encoding was required and instead the orientation discrimination was performed immediately. This result was complemented by significantly elevated activity relative to baseline during the delay period in the FEF and aIPS, but no evidence of this pattern in the IFJ, implicating the former regions in working memory maintenance. Finally, the authors also used Granger causality to model the effective connectivity between the IFJ, FEF and aIPS. They showed that IFJ activity during working memory encoding predicts activity in the FEF and aIPS during the maintenance phase and therefore suggested that the IFJ is involved in sending top-down signals to these regions to initiate working memory maintenance processes. Despite being limited by some of the intrinsic weaknesses of the Granger causality analysis (Seth et al., 2015), this study was to the best of our knowledge the first that using this technique reported directed interactions between the IFJ and FEF during the performance of a feature-based working memory task. Finally, Zhang et al. (2018) performed two fMRI experiments using feature-based attention tasks on colour and motion stimuli to investigate the source(s) of the spatially global effect of feature-based attention on visual activity (shown in Figure 2e). In their paradigm, subjects were cued to attend either the colour (red/green) or the motion

(upward/downward) of a group of dots displayed in the left or the right visual hemifield, while ignoring the dots on the other (which could share the attended feature or not). The authors also ran two localizer tasks at the beginning of each experiment and used a general linear model to identify the ROIs activated by the stimulus type (V4 for colour features and MT+ for motion features) and by the blocked experimental task (feature-based task vs. control task, activating the IPS, FEF, IFG and the medial frontal gyrus). They showed that V4 and MT+ activity was significantly elevated when they presented a matching feature to the one attended in the to-be-ignored visual hemifield compared with a mismatching one. This result thus replicated the classic global effect of feature-based attention (Serences & Boynton, 2007). Then, the authors used dynamic causal modelling to evaluate 15 different models that could potentially account for feature-based modulatory effects on neural activity in the ‘same’ condition in each participant. By comparing the exceedance probabilities (computed using a Bayesian hierarchical approach) of each model, they revealed that a model with feedback modulation from IFJ to V4 and MT+ (which interestingly was also enhanced in the contralateral compared with the ipsilateral hemisphere) was better able to account for the results of both Experiments 1 and 2, respectively. A converging interpretation was also suggested by the fact that the attention modulation index correlated significantly with the effective connectivity strengths from the IFJ. In an additional control analysis that also used dynamic causal modelling, by evaluating several families of models, the authors showed that signals recorded in the IPS, FEF, IFG and the medial frontal gyrus were also driven by the modulation from the IFJ, thus excluding the possibility that the effects on V4 and MT+ could be due to a third node of the network. They complemented this analysis by Granger causality measures, which in contrast to dynamic causal modelling (that requires the specification of a priori ROIs), can be used as a fully data-driven technique. This showed that the IFJ was the node with the greatest outflow and net-flow degree, whereas V4 and MT+ were the nodes with the greatest inflow. In summary, by combining the accurate localization of the ROIs with the analysis of their effective connectivity, this study presents compelling evidence that the IFJ can be considered as the source of the global effect of feature-based attention.

Taken together, the studies reviewed thus far point to an involvement of the IFJ in both feature-based attention and working memory, but can the IFJ be considered part of a purely non-spatial system? For this to be the case, evidence that attentional selection in the IFJ operates at the level of whole objects (i.e., as object-based attention) is crucial. As we have seen, disentangling non-spatial processes at the behavioural level requires sophisticated experimental techniques and designs that render spatial information irrelevant during the execution of the task. Furthermore, studying object-based control processes requires also ruling out the possibility that the participants could rely on low-level features to perform the task. In this sense, the study by Liu (2016) was designed to explicitly test and isolate neural processes related to purely object-based attentional selection. In the experimental paradigm of this study, participants were presented with superimposed visual stimuli (Gabor patches) that simultaneously changed in spatial frequency, orientation and colour, thus making both spatial- and feature-based selection ineffective for task completion (see Figure 2g). At the beginning of each trial, one of the patches was cued, and the subjects had to track it to perform a change detection task. By using MVPA on the trials in which the subjects did not

make a response (to exclude motor and decision-making components), the study showed that the attended object could be decoded above chance in the bilateral IFJ, FEF and aIPS, providing evidence of purely object-based priority signals in these regions.

Critically, even though all the regions reported in most of the previous studies (i.e., the IFJ, FEF and IPS) are implicated in top-down modulation, measuring the temporal profile of their involvement in spatial and non-spatial processes is crucial to firmly establish which are the sources of the modulation within the attention networks. In contrast to fMRI, MEG is ideally suited to measure neural activity with a high temporal resolution and to reveal the statistical interdependence of signals originating from different cortical sources (see Gross, 2019, for a recent discussion of MEG unique strengths). Furthermore, combining the spatial accuracy afforded by fMRI localization techniques with MEG by reconstructing a realistic head model of the subjects, and mapping the magnetic signals to the source space by computing the inverse solution, arguably represents the most detailed non-invasive method to measure ongoing prefrontal activity in human subjects. Baldauf and Desimone (2014) used precisely the combination of these two methodologies (i.e., fMRI and MEG) to uncover the role of the IFJ in object-based attention. In their paradigm, the participants were instructed to detect the repetition of a target presented among superimposed pictures of faces and houses (Figure 2i). The task was a one-back repetition, and the participants were cued about which type of stimuli they had to attend (face vs. house) at the beginning of each trial. The stimuli were presented rhythmically at 2 and 1.5 Hz, respectively, by manipulating their phase using a phase-scrambling technique, thus generating two overlapping streams of frequency-tagged objects. The authors capitalized on this feature of their experimental design to investigate the coherence between the source and the target nodes of top-down object-based attentional modulation. Firstly, they identified the ROIs that were involved in face and house processing (the fusiform face area [FFA] and the parahippocampal place area [PPA], respectively) and spatial, feature- and object-based attention (the FEF and IFJ, respectively) by running three different blocked-design fMRI localizer tasks. The ROIs obtained by this procedure were then projected on the native cortical surface to analyse MEG signals in source space. Their results showed that, when attending to the preferred stimulus, FFA and PPA increased their coherence with the IFJ in the tagging stimulus frequency and also in the gamma frequency band (60 to 90 Hz), although the specific peak varied considerably between subjects. Furthermore, in nine out of the 12 subjects, the phase lags between the IFJ and FFA and PPA increased linearly depending on the frequencies, suggesting that IFJ cyclic responses were the driver of FFA and PPA responses to the stimuli with an approximate lag of 20 ms (which is presumably due to signal's transmission time). This interpretation is consistent with the communication through coherence framework (Fries, 2005), which postulates that transmitted spikes need to arrive at the right time in order to render the communication between areas effective (within windows of opportunity; that is, periods of maximal depolarization). According to the authors, the IFJ would be indeed best suited to bias neural activity in object identification modules in the temporal lobe by coupling its activity with these sites depending on the task requirements, in a remarkably similar manner to the FEF shifting spatial attention towards different spatial locations.

In the study by Nee and D'Esposito (2016), which innovatively related the IFJ to general principles of functional organization in the PFC (e.g., Koechlin et al., 2003), the authors orthogonally manipulated task demands related to stimulus domain, contextual and temporal control, to engage three main sections of the IPFC (defined rostral, mid and caudal). Their univariate fMRI results revealed that the contextual and stimulus domain manipulation activated the left IFJ but that rostral areas were exclusively employed by the temporal manipulation, reflecting an increased abstraction level in the control of behaviour by these three subregions. Subsequently, they analysed whether, and at which level of the rostro-caudal axis, stimulus sensitivity emerged. In the caudal PFC, particularly, the dorsal parts (SFS and cMFG) were sensitive to spatial information, whereas the ventral parts were more sensitive to verbal information (IFJ and IFS), but the rostral regions did not show this pattern. Finally, dynamic causal modelling revealed that the mid regions of the IFJ had a stronger efferent connection to both rostral and caudal ones, rather than vice versa, thus positioning them at the apex of the IPFC hierarchy. These results are particularly relevant because they again demonstrate a robust stimulus domain sensitivity in the pIPFC and also clarify the directed influence of more rostral sites (i.e., the cMFG and the IFS) to the SFS and IFJ, which may be involved in more integrative cognitive processes, such as spatial and object-based working memory, and the executive control of action.

We would like to conclude this section by discussing two recent studies on the role of the IFJ in non-spatial attention. Gong and Liu (2020) investigated whether the IFJ encodes information about the attended feature itself (e.g., which colour is currently attended) using MVPA. In a large sample of 48 subjects, they found that the bilateral IFJ contains a neural representation of the currently attended visual feature. Employing compound stimuli, which consisted of two orthogonal features (i.e., red vs. green colour and clockwise vs. counterclockwise motion), they were able to show that the IFJ had a bias to consistently encode the attended feature better than the unattended. Similarly, Meyyappan et al. (2021) studied the role of the IFJ in feature-based attention but, most importantly, directly contrasted its involvement in non-spatial attention to visual features with its involvement in spatial attention by including both forms of top-down control within a single paradigm. By analysing fMRI activity in individual trials with univariate general linear models and MVPA, they found that the univariate BOLD activity showed no difference in pIPFC between feature-based and spatial-based attention. However, the MVPA classifier revealed significant decoding accuracy of feature attention in the bilateral IFJ, while the same structure did not encode sufficient information about spatial attention in order to allow above-chance level classification of the attended location. To explain these results, the authors propose a model in which (the right) IFJ guides feature-based attention but not (covert) spatial attention during the cue-target interval.

In summary, although the recent neuroimaging studies that were in part influenced by the hypothesis of spatial versus feature and object selectivity in the pIPFC present a more nuanced view of this segregation in the FEF and IFJ, they nevertheless confirm the overarching idea (mainly, thanks to the improvements in data analysis techniques, such as MVPA) that the former is predominantly involved in processing spatial information, whereas

the latter is predominantly involved in processing non-spatial information. Moreover, functional and effective connectivity metrics revealed that the coordination of spatial and non-spatial selection requires the communication between the FEF and IFJ and posterior areas, in which the FEF assumes the role of a spatial ‘priority map’, whereas the IFJ biases non-spatial visual processing and acts more as a control structure that allocates attentional resources depending on the task at hand in a flexible way. An interesting question to address seems therefore whether the role of the IFJ in cognition is more multifaceted than the role of the FEF, which could be thought of as more specialized. This would seem reasonable from a comparative perspective because the PFC and the information processing stream in which the IFJ is hypothesized to be embedded (O’Reilly, 2010) is one of the brain districts where humans diverge the most from other primates in terms of its size and relative organization (Donahue et al., 2018; Eichert et al., 2020; Kravitz et al., 2013; Mars, Sotiropoulos, et al., 2018). In the next section, we will attempt to expand on this view by discussing it in the light of the multiple-demand system hypothesis (Duncan, 2010).

2.3.4 | Multiple-demand system (inclusion in the multiple-demand system)

In its essence, the multiple-demand hypothesis is built around the idea that a limited set of brain regions are all involved in many aspects of high-level, goal-driven cognitive processes that collectively give rise to intelligent behaviour. The primary sources of empirical support for this hypothesis (together with single-cell recordings in primates) are fMRI studies that identified overlap in frontal and parietal regions between the activity elicited by a wide range of tasks and resting-state functional connectivity patterns (Duncan, 2010). Traditionally, the prefrontal areas that are thought to be part of the multiple-demand system are localized within and posterior to the IFS, thus likely encompassing the IFJ (Duncan, 2010; Fedorenko et al., 2012). Fedorenko et al. (2013) tested the hallmark of the multiple-demand hypothesis by measuring brain activity using fMRI in several diverse experimental paradigms, which included reading sentences and non-sentences, performing a memory-probe task (used as localizer in all the subjects) and optionally performing one or more of the following tasks: a spatial and verbal working memory task, a Stroop task, two versions of the multisource interference task and an arithmetic task. Each task was administered in an easy versus hard version in a blocked experimental design. Crucially, all the analyses were performed in the native subject space to directly probe the degree of overlap in the activations elicited by these paradigms. The results clearly showed that a set of frontal and parietal regions is consistently activated by the global contrast of the respective hard versus easy task versions. Of interest to the scope of the present review, the activations were found all along the premotor regions of the precentral gyrus, in the MFG and in the posterior IFG. It is important to note that although this pattern of activation is consistent with the multiple-demand system hypothesis, the authors left open the possibility that other dissociations exist among the regions that form part of this system. In support of this possibility, the study by Noyce et al. (2017) attempted to reconcile the multiple-demand account with the results by Michalka et al. (2015); reviewed in Section 2.3.1) that reported the existence of sensory selectivity in the IPFC. In their fMRI study, they used two visual and auditory two-back tasks to probe IPFC responses in a new paradigm modified and adapted

from the study by Michalka et al. (2015). With this, they indeed replicated and extended their original finding of four interleaved visual and auditory sensory regions in the IPFC. By leveraging the fact that seven subjects participated in the previous study, they also computed a Dice coefficient on the activations found in the present study, which all had significant spatial overlap (ranging between 0.57 and 0.7). Finally, by averaging visual and auditory activation and contrasting them with the averaged sensorimotor control activation patterns, the authors introduced the concept of a degree of multiple-demand responsiveness. This degree spanned from areas that did not show any sensory bias, but only working memory activation, in the anterior insula cortex and in the dorsal anterior cingulate cortex/pre-supplementary motor area (thus labelled ‘pure’ multiple-demand areas), to areas showing a bias towards visual modality, but also increased activation in the working memory task in their non-preferred modality (i.e., with auditory stimuli) in the iPCS and the right sPCS (therefore considered ‘partial’ areas). These results are particularly interesting in that they show that the iPCS and sPCS (which are the closest anatomical landmarks to the IFJ and FEF, respectively; see Section 2.2.2) encode sensory-specific visual information but that they may as well process general domain signals that globally support attention and working memory functions (Noyce et al., 2017).

In the study by Muhle-Karbe et al. (2017), the authors investigated the encoding of novel task instructions (i.e., the task set) and its relationship to the multiple-demand system. In particular, their fMRI study aimed to measure activations during the delay period to disentangle activity related to the preparation of novel stimulus-response mappings from their simple memorization. The participants were instructed to respond to face and house stimuli by pressing a button with their index or middle finger, or to simply report whether a probe contained matching or mismatching instructions compared with the initial display shown before the delay period. The decoding accuracy of brain activity using MVPA was higher than chance during the delay period in the blocks requiring the implementation of novel stimulus-response mappings and significantly increased compared with the memorization blocks in the IFJ, the FFA and the PPA. Thus, these results argue in favour of a role of the IFJ in encoding abstract task rules (in this case, stimulus-response mappings) and in the maintenance of working memory representations, which were less accurately decoded in this study, although they were also likely contributing to the overall activation patterns.

Finally, in the most comprehensive analysis of the multiple-demand system available to date, Assem et al. (2020) combined the accurate alignment of cortical areas across subjects using improved registration methods (Robinson et al., 2014) with the parcellation of the individual cortex using the MMP1 by Glasser et al. (2016) in a very large sample of subjects ($n = 449$ subjects from the Human Connectome Project; Van Essen et al., 2013) to answer five core questions of the multiple-demand hypothesis (we will focus here only on the delineation of the multiple-demand system; the reader is referred to the original publication for further details). By performing a conjunction analysis on three fMRI tasks that should activate the putative multiple-demand regions (viz., a working memory n-back task, a relational reasoning task and a math/story task), the authors identified areas that formed part of the ‘penumbra’ and the ‘core’ multiple-demand system by computing the parcels that had

stronger mean activations compared with the initial 27 parcels of the ‘extended’ multiple-demand system. Interestingly, both the area IFJp (activated by the relational reasoning and the math task contrasts) and the area i6-8 (activated by all three task contrasts and preferentially by the working memory task) that lies immediately anterior to the FEF were included in the core multiple-demand system. An additional analysis using contrasts with weaker cognitive demands in the working memory and relational reasoning tasks identified additional foci in the FEF and anterior IFJ (IFJa), among others. This suggests that these regions may display partial multiple-demand characteristics and that this possibility may need further scrutiny. However, as shown by the analysis of resting-state functional connectivity, the core regions were more strongly interconnected, and all belonged to the frontoparietal network (Ji et al., 2019), confirming the reliability of the multiple-demand system delineation proposed by the authors.

In conclusion, several papers have now reported the involvement of the IFJ in the multiple-demand system, thus reinforcing the hypothesis that this area may have a broader role in cognition compared with the FEF. This idea is consistent with the view that the visuospatial attention system is evolutionarily older and its organization is well preserved in primates (Caminiti et al., 2015), whereas the vlPFC, and its projections to the temporo-occipital cortex, might underlie the emergence of more complex human behaviours (Eichert et al., 2020; Mars, Sotiropoulos, et al., 2018; Neubert et al., 2014).

2.4 | CONNECTIVITY FINGERPRINTS

We began the present review by introducing the hypothesis that the function of a brain region is ultimately determined by its intrinsic and extrinsic connectivity fingerprints and its structural properties (Passingham et al., 2002). At a time in which network neuroscience has become so prominent, we would almost take this hypothesis to be self-evident. However, it wasn’t until recently, with the advent of big data approaches (thanks to the availability of extensive neuroimaging public datasets and repositories; e.g., Van Essen et al., 2013), that this hypothesis could be experimentally tested (Mars, Passingham, & Jbabdi, 2018). This section will thus focus, wherever feasible, on such approaches aggregating large amounts of multimodal neuroimaging data to model the structural and functional connectivity of the plPFC. Furthermore, an appropriate emphasis will be put on comparative evidence, particularly in the case of non-invasive methodologies that allow inferring brain connectivity but have not been thoroughly validated yet (i.e., diffusion magnetic resonance imaging [dMRI]; Donahue et al., 2016; Maier-Hein et al., 2017; van den Heuvel et al., 2015). In the following sections, we will discuss studies that adopted a seed-based approach to analyse specific ROIs connectivity to answer well-defined research questions about the structural and functional connectivity of the plPFC.

2.4.1 | Structural connectivity

In contrast to non-human primates, and in particular, the macaque, in which the tracer studies performed in the last decades have enabled the detailed mapping of the brain’s architecture and structural connectivity of this species (Barbas & Pandya, 1989; Felleman &

Van Essen, 1991; Kötter, 2004; Markov et al., 2014), in humans, this knowledge is predominantly based on dMRI (Jeurissen et al., 2019). Although this methodology has held the promise of revealing non-invasively the structural connectivity and white-matter structures of the human brain at a level of detail comparable with invasive and *ex vivo* studies, it is still affected by biases, false positives and common methodological misconceptions in the research community itself (Jeurissen et al., 2019; Maier-Hein et al., 2017). These limitations notwithstanding, it has also allowed researchers to probe the structural connectivity of large populations with a variety of algorithms to investigate a growing set of measures related to major white-matter bundles, local tissue properties and further down to tissues microstructure. In addition, the combination of dMRI with fMRI allows researchers to investigate the structural connectivity of functionally defined seeds and its relationship to functional connectivity, based on the idea that the underpinning of functional connectivity lies in structural connectivity. Although this relationship is difficult to establish due to inherent methodological limitations and it is certainly still controversial, some studies that combined these methods have shown remarkable results in how structural connectivity can be used to predict task-fMRI activations in several specialized brain modules (Osher et al., 2016; Saygin et al., 2012).

In terms of our knowledge of the structural connectivity of the plPFC, as mentioned earlier, comparative evidence provides a solid foundation against which dMRI results in humans can be usefully related (Schall et al., 1995; Stanton et al., 1995; Webster et al., 1994; Yeterian et al., 2012). In one of the earliest comparative dMRI studies, Croxson et al. (2005) described the structural connectivity of the human PFC using probabilistic tractography (Behrens et al., 2003) and compared it with the macaque's, revealing striking similarities in the structural connectivity patterns in the two species. The following studies have primarily focused on establishing a relationship between the PFC association tracts (Croxson et al., 2005) and subregions involved in specific functions, among which visuospatial attention. In an outstanding contribution to the understanding of the structural underpinnings of visuospatial selection, de Schotten et al. (2011) initially compared the organization of the three branches of the superior longitudinal fasciculus (SLF) in the rhesus macaque (atlas-based) and humans ($n = 20$; for which they had also available *ex vivo* data from a single subject as ground truth) by performing the virtual dissection of this bundle (Figure 3a). The authors moreover identified the cortical terminations of the SLF and their relationship with the functional activation profiles of the DAN and VAN originally proposed by Corbetta and Shulman (2002). From their study, it emerges that the FEF is reached by the cortical terminations of the SLF1 and SLF2. In contrast, the IFJ is mostly reached by the terminations of the SLF2 and SLF3 (even though it is important to note that in this study these ROIs were only defined at the group level), potentially highlighting a dissociation in the macroscale anatomical connectivity of these two areas. In Umarova et al. (2010), the authors combined fMRI—employed to define the nodes involved in visuospatial processing using an endogenous cueing task—with probabilistic tractography, to analyse their reciprocal structural connectivity in 26 participants. This study showed that, in the right hemisphere, the FEF is wired through the SLF2 to the temporoparietal cortex, revealing a dorsal white-matter pathway from the FEF passing within the inferior parietal lobule to the IPS, the

supramarginal gyrus, the caudal superior temporal gyrus and V5/MT+. The study by Anderson et al. (2012) employed a similar logic to measure the structural connectivity between the nodes involved in oculomotor control, including the FEF, the supplementary eye field and the premotor eye field. These nodes were defined using an fMRI localizer task that consisted of alternating blocks of voluntary horizontal saccades performed in darkness and fixation blocks. The reconstructed streamlines from the FEF showed terminations in the inferior parietal cortex (the anatomically defined IPS1, IPS2 and IPS3), with a higher streamline count in the right hemisphere, potentially suggesting right lateralization of this pathway. Although one limitation of this study is that the tractography model adopted was a deterministic one, these results fit well with the study by Umarova et al. (2010). Moreover, they are consistent with the available evidence in macaques (in particular, of a pathway connecting the FEF with the lateral intraparietal area, the putative homologue of the IPS in humans; Stanton et al., 1995). Finally, Szczepanski et al. (2013) aimed at distinguishing the contribution of DAN nodes to viewer- and object-centred processes (these nodes were defined using a memory-guided saccade topographic localizer fMRI task). By analysing dMRI data using probabilistic tractography, they showed that the FEF was more likely connected with IPS2 than with SPL1. Vice versa, the supplementary eye field was more likely connected with SPL1 than with IPS2. Their study provides evidence for a model in which FEF-IPS2 structural and functional connectivity support viewer-centred processing, whereas the supplementary eye field-SPL1 structural and functional connectivity support object-centred processing, therefore effectively dissociating gaze- and object-centred representations. In summary, the reviewed evidence on the FEF suggests that this region exhibits reproducible patterns of structural connectivity with the parietal lobe and particularly with the IPS complex. As we have already reviewed in Sections 2.3.1 and 2.3.2, the IPS belongs to the DAN, and it is also topographically organized, while being often proposed as the locus of a priority map of space, similarly to the FEF (Fecteau & Munoz, 2006).

Unfortunately, the seed-based structural connectivity analysis of the IFJ suffers from a remarkable lack of data. Moreover, to the best of our knowledge, no publication reported evidence on the structural connectivity of the functionally defined IFJ. Baldauf and Desimone (2014) analysed the structural connectivity of the FFA and PPA (localized using fMRI) using probabilistic tractography. They then used the outputs to classify subregions in the PFC based on their probability values. The authors were able to show that the regions that display a higher likelihood of being structurally connected with the FFA are localized in the vicinity of the IFJ, in the pars triangularis, the pars opercularis and the cMFG. However, the extrapolation from these results of structural connectivity patterns in the opposite direction (viz., from the IFJ to FFA and PPA) is prevented by the fact that probabilistic tractography results are strongly affected by the location where the streamlines are initialized to propagate. Thus, evidence from the seed-based analysis of the structural connectivity of the IFJ is needed to complement these findings. Finally, the authors also used a deterministic tractography algorithm to perform a virtual dissection of the white-matter bundles that connect the PPA and the FFA to the pars opercularis (which includes part of the IFJ) and suggested that the uncinate fasciculus underlays these structural connectivity pathways.

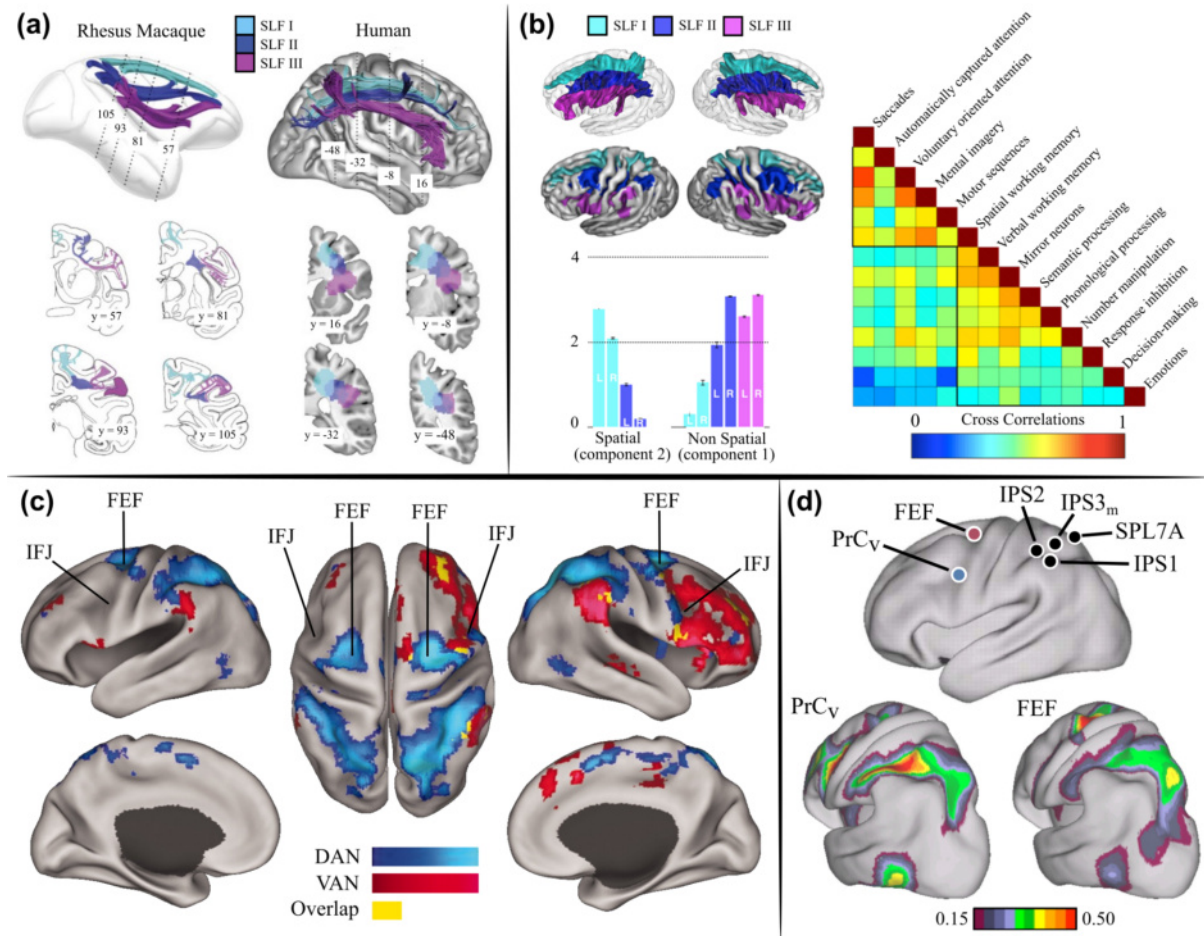


FIGURE 3 Structural connectivity and resting-state functional connectivity of the posterior lateral prefrontal cortex. (a) depicts the comparison between the organization of the three branches of the superior longitudinal fasciculus (SLF) in macaques and humans. This frontoparietal bundle was delineated using a virtual dissection protocol in 20 adult participants (adapted from de Schotten et al., 2011). (b) presents a summary of the findings from the study by Parlatini et al. (2017). The activation maps resulting from an fMRI meta-analysis of 14 distinct cognitive functions were clustered using a principal component analysis in a ‘spatial/motor’ and a ‘non-spatial/motor’ component (b, right side). These maps’ z scores were related to the cortical terminations of the three branches of the SLF obtained from a large sample of participants ($n = 129$), suggesting that the SLF1 could preferentially mediate ‘spatial’ processes, whereas the SLF3 could preferentially mediate ‘non-spatial’ processes. The SLF2 overlapped with both activation components, therefore possibly underlying their interactions (b, left side). (c) The dorsal and the ventral attention networks identified for the first time during resting-state fMRI in the study by Fox et al. (2006). These spontaneous activity patterns show high resemblance to the two attentional systems proposed by Corbetta and Shulman (2002) and highlight the potential of resting-state data to reveal stable modes of organization of the attention networks in the absence of task demands (see also De Pasquale et al., 2010, for converging evidence on the organization of the DAN using MEG). (d) Seed- based analysis of resting-state fMRI functional connectivity of the FEF and

the ventro-caudal prefrontal region (PrCv) from the study by Yeo et al. (2011). The authors defined the former nodes by performing an fMRI meta-analysis and using a separate discovery sample, respectively, and employed a data-driven approach to probe their connectivity patterns. In a subsequent stage, they tested them in an independent replication sample in a confirmatory fashion. They found that within the posterior parietal cortex, the medio-caudal SPL showed increased functional coupling with FEF, whereas the lateral IPS complex showed increased functional coupling with PrCv in their replication sample. These results suggest segregated parallel pathways from the plPFC to the SPL and the IPS complex

Finally, one of the most significant contributions to the characterization of the relationship between the structural connectivity and the function of the plPFC can be found in the study by Parlatini et al. (2017). The authors combined the fMRI meta-analysis of 14 different cognitive domains with the virtual dissection of the SLF in a large sample of participants ($n = 129$; Figure 3b). The study aimed to reveal how the three branches of the SLF relate to the functional specializations of the areas that belong to the frontoparietal network. Importantly, the virtual dissection of the SLF was performed using a modified version of spherical deconvolution (Dell'Acqua et al., 2010), which allowed it to preserve its organization in three distinct branches, despite the presence of crossing fibres near the corona radiata. In their meta-analysis, the authors clustered frontoparietal regions' co-activations into two components using a principal component analysis. This analysis revealed that two components, referred to as a 'spatial/motor' component and a 'non-spatial/motor' component, were together able to account for 70% of the co-activation data variance. Crucially, the average z scores (thresholded at 50%) of these components differentially loaded on the SLF1 and SLF3 cortical terminations, respectively. The SLF2 terminations instead overlapped with both components (for which the shared activations were mainly localized within BA6 in the PFC), and this bundle was therefore suggested to underlie the interactions between these two functional components. Based on the figures from this study (in particular, fig. 6; shown in the left middle row of Figure 3b), we speculate that the IFJ may be localized near SLF2 and SLF3 terminations, thus suggesting anatomical pathways through which the IFJ could mediate 'non-spatial/motor' functions. We therefore propose that future studies should specifically address the question of how the cortical terminations of the three branches of the SLF relate to functional subdivisions of the PFC.

2.4.2 | Resting-state functional connectivity

One of the major breakthroughs in the study of the brain networks involved in visual attention has been the observation that the coupling between BOLD activity in different brain regions measured during the performance of attentional tasks is preserved in resting-state conditions (Fox et al., 2006; Figure 3c). These spontaneous activity patterns again confirmed the existence of a bilateral DAN (with the FEF and IPS as main nodes) and a right-lateralized VAN (with the ventral frontal cortex and TPJ as main nodes). Due to the overlap of activations in the right MFG and IFG, Fox et al. (2006) suggested that these nodes could mediate the interaction between the DAN and VAN. Importantly, in a subsequent study by De Pasquale et al. (2010), the authors used fMRI coordinates to define the DAN nodes in MEG

source space and validated the segregation of this network and its correspondence with the network isolated by resting-state fMRI. Such multi-modal combinations highlight the potentiality of MEG to characterize the spectral characteristics of resting-state networks and their temporal dynamics (De Pasquale et al., 2010). Therefore, one of the most intriguing questions is how spontaneous neural activity (as measured with fMRI or MEG) could provide a window into the reciprocal interactions and the functional differentiation of the FEF and IFJ. Furthermore, it would be fascinating if such resting-state activations can be used to subdivide the attention networks at an even finer grain, for instance, by stimulus domain (i.e., spatial vs. non-spatial), rather than the more prevalent top-down versus bottom-up functional dichotomy (Corbetta & Shulman, 2002).

An alternative classification of the resting-state network organization of the plPFC was presented in the fMRI study by Cole and Schneider (2007). To define their ROIs, the authors used a modified search task that entailed working memory encoding and maintenance while allowing the separation of these processes from stimulus-response mapping. They subsequently analysed the functional connectivity between these previously defined six bilateral ROIs, including the IFJ and dorsal premotor cortex, in resting-state conditions. They showed that these nodes had higher functional connectivity than six different nodes engaged in domain-specific processes, highlighting a cognitive control network (Cole & Schneider, 2007). In a similar vein, Vincent et al. (2008) analysed the seed-based functional connectivity of the anterior PFC to probe whether this region belongs to an anatomically segregated control network that could mediate the communication between the anti-correlated DAN and the hippocampal-cortical memory system (a component of the default mode network). A remarkable methodological strength of this study is that the bilateral aPFC network was delineated in a first dataset ($n = 10$), but the remaining seeds (MT+ and the hippocampal formation) were defined through a correlation analysis in a second dataset, and finally that the segregation of the networks was tested in a yet third, independent dataset ($n = 50$ and $n = 45$). The authors were able to show that a frontoparietal network is interposed between the DAN and the hippocampal-cortical memory system with minimal overlap. An important refinement of the proposed role of the frontoparietal network was formalized by Cole et al. (2013). The authors of this study tested participants in a variety of fMRI tasks involving the implementation of novel instructions and showed that the frontoparietal network exhibited two general properties that are consistent with its role as a flexible hub network: (1) greater global variable connectivity compared with the other resting-state networks and (2) compositional coding of information as reflected in its activity patterns during task performance. Following this evidence, and the studies reviewed in Section 2.3.4, it would seem reasonable to implicate the IFJ in the frontoparietal network, in accordance with its role as an executive control structure that belongs to the multiple-demand system (Assem et al., 2020).

In one of the most influential resting-state fMRI network parcellation (Yeo et al., 2011; $n = 1000$), the FEF (as defined through an fMRI meta-analysis) was reported to be part of the DAN and showed increased functional connectivity with the caudal IPS and SPL, whereas the ventro-caudal frontal region (termed the PrCv, and defined in an independent

fMRI ‘discovery sample’; Yeo et al., 2011; likely encompassing the IFJ), which was also part of the DAN, showed increased functional connectivity with ventral parts of the rostral IPS and SPL (Figure 3d). In their replication sample, the authors again found evidence of increased functional coupling between FEF and the medio-caudal SPL and between PrCv and the rostro-lateral IPS complex. This combination of a data-driven and a confirmatory approach represents a powerful methodology to uncover novel organizational principles of functional interactions between the PFC and posterior areas. Finally, according to the recent resting-state fMRI network partition by Ji et al. (2019; whose nodes are in turn based on the MMP1 parcellation), the FEF is part of the cingulo-opercular network, and the IFJp is part of the frontoparietal network, whereas the IFJa is part of a newly defined language network.

2.4.3 | Meta-analytic connectivity modelling

The plPFC engages with multiple regions dispersed all over the brain, making the process of reporting its co-activation patterns in all possible experimental scenarios a daunting task. However, thanks to the technique known as meta-analytic connectivity modelling (MACM; Robinson et al., 2010), the results from multiple fMRI experiments involving a common seed region can be efficiently summarized, used to probe specific hypotheses about regional segregation and made accessible to the neuroscientific community. In the last decade, several studies have used this meta-analytic technique to model plPFC co-activations, including the FEF and IFJ. Sundermann and Pfliegerer (2012) published one of the most detailed analyses of the functional connectivity of the IFJ, combining an ALE, MACM and an independent resting-state fMRI analysis. The authors used the coordinates provided in Derrfuss et al. (2005) to retrieve from the BrainMap database (<http://brainmap.org/>) all the foci that were co-activated with the putative IFJ seed, in a way that effectively makes their ROI definition agnostic for anatomical descriptors and functional specialization of this region. Their MACM results (which were drawn from 180 experiments for the left IFJ and 131 for the right IFJ) reveal that the IFJ is robustly co-activated with the dlPFC and the vlPFC, the MFG/pre-supplementary motor area, the anterior insula, the posterior parietal cortex and the occipitotemporal junction, among others. The authors interpret these findings as largely consistent with the proposal advanced by Cole and Schneider (2007) that identifies the IFJ as one of the crucial nodes of the cognitive control network, an interpretation that was further supported by the resting-state fMRI analysis (Sundermann & Pfliegerer, 2012). In Muhle-Karbe et al. (2016), a data-driven seed-based parcellation was performed on the IPFC using k-means clustering. The activation patterns of the six ensuing clusters were characterized using MACM. Cluster 1, localized at the intersection of the iPCS and the IFS, matched the IFJ coordinates reported in previous studies (Derrfuss et al., 2004, 2009) and co-activated with the rIFJ, lIPS, right anterior insula and bilateral pre-supplementary motor area. In a follow-up study by Ngo et al. (2019), the authors applied the author-topic model (https://github.com/ThomasYeoLab/Ngo2019_AuthorTopic) to find sub-components in the co-activation patterns of the left IFJ cluster reported in the previous study by Muhle-Karbe et al. (2016). They showed three main components that could describe these patterns: a first component related to language processing, a second component involved in attentional control and a third one, which they speculated may reflect

inhibition and response conflict resolution. Of interest to our present purpose, the second component engaged the bilateral IPS and SPL, which seems to fit the functional role attributed to this co-activation pattern. Thus, in addition to the analytic solution afforded by MACM, the author-topic models represent a viable and promising approach to fractionate the functional domains in which the IFJ is involved and could, for example, be used to contrast the function of the IFJ in the two hemispheres.

Perhaps because of its more consensually established functional role, the only study that we are aware of providing evidence on the FEF co-activation patterns is the one by Cieslik et al. (2016). The authors combined a coordinate-based meta-analysis and MACM to dissociate the oculomotor regions involved in anti-saccade and pro-saccade task performance (Cieslik et al., 2016). The lateral FEF was identified through an ALE meta-analysis focusing on pro-saccade versus baseline/ fixation fMRI contrasts, whereas the medial FEF was identified by anti-saccade versus pro-saccade contrasts. Interestingly, these contrasts identified some regions of overlap but also showed that these two foci of activation were partially dissociable. In turn, MACM revealed that the lateral FEF showed increased functional connectivity with motor regions, whereas the medial FEF showed distinct functional connectivity patterns that were related by the authors to the multiple-demand system (Fedorenko et al., 2013). While these results are certainly intriguing, one limitation of the study is that the coordinate-based meta-analysis was underpowered; hence, the hypothesis of segregation of the FEF based on the involvement in anti-saccade and pro-saccade performance needs to be further explored in future studies. To conclude, in this section, we reviewed several metrics of brain connectivity, including structural connectivity as inferred from dMRI, functional connectivity during resting state measured using fMRI and MEG, and MACM. These metrics suggest that the FEF displays robust structural connectivity patterns with the IPS complex, consistent with comparative evidence, whereas the structural connectivity of the IFJ remains largely unexplored. During resting state, FEF activity forms the backbone of the DAN (along with IPS and MT+) in both fMRI (Fox et al., 2006; Yeo et al., 2011) and MEG (De Pasquale et al., 2010), whereas IFJ activity patterns seem to be better characterized as belonging to a frontoparietal (alternatively, a cognitive control) network (Cole & Schneider, 2007; Ji et al., 2019). Resting-state MEG could be therefore used to measure IFJ dynamic functional connectivity to assess the robustness of its assignment to this network over time. The IFJ similarly co-activates with overlapping regions of the frontoparietal network in a variety of tasks as revealed by MACM, but the author-topic model (Ngo et al., 2019) suggests that these co-activation patterns underlie at least three different cognitive subcomponents. We propose that the convergent application of these techniques to the study of the FEF could be used to differentiate its cognitive subcomponents and to potentially compare the topography of its co-activation patterns in attentional control tasks with the ones previously reported in the IFJ (Ngo et al., 2019).

2.5 | GENERAL DISCUSSION AND FUTURE DIRECTIONS

In the present review, we discussed recent neuroimaging evidence suggesting that although the FEF and IFJ are implicated in similar and overlapping cognitive functions, they

have remarkably distinct roles in shaping goal-driven behaviour (Baldauf & Desimone, 2014; Tamber-Rosenau et al., 2018; Zanto et al., 2011; Zhang et al., 2018). These differences are not apparent when considering their structure, localization, selectivity to sensory modalities or their functional specialization alone, but only when the broader spectrum of their activation in response to attentional, working memory and executive tasks, and crucially, their connectivity fingerprints (Mars, Passingham, & Jbabdi, 2018; Passingham et al., 2002) are considered. This likely reflects the intrinsic difficulty of identifying functional specializations in regions that in primates are by nature flexibly engaged in a variety of high-level cognitive mechanisms (Duncan, 2010; Fuster, 2001; Goldman-Rakic, 1996; Miller & Cohen, 2001). Taken together, the studies reviewed indicate that when we compare the FEF and IFJ on these broader aspects, these regions' functional roles and connectivity differ considerably. Our main results are summarized in Table 2 for each of the aspects that were contrasted in this review, along with the main references consulted.

Table 2 Summary of the main findings reviewed

Domain	Section title	Summary of the findings	Main references
Structure	Cyto-, chemo- and receptorarchitecture	The cytoarchitecture of the FEF is dysgranular. This region is part of BA 6, and, to a lesser extent, of BA 8. Its chemoarchitecture segregates it from the superior and the middle frontal gyrus. The cytoarchitecture of the IFJ is also dysgranular. This region lies in BA 6, BA 8, and BA 44. Its receptor fingerprint segregates it from the ventral 44d. Receptorarchitecture also allows to segregate the IFJ in two distinct subregions.	Amunts et al. (2010); Amunts and von Cramon (2006); Petrides and Pandya (1999, 2002); Rosano et al. (2003); Zilles and Amunts (2018).
Structure	Localization and relation to sulcal morphology	The FEF is localized ventral to the junction of the sPCS and the SFS. The IFJ is localized dorsal to the junction of the iPCS with the IFS.	Amiez et al. (2006); Derrfuss et al. (2009, 2012); Koyama et al. (2004).
Function	Sensory domains (sensory vs supra-modal coding) and topographic organization	The FEF and IFJ are both primarily selective for visual information, but only the FEF contains a full topographic map of contralateral space.	Hagler and Sereno (2006); Kastner et al. (2007); Mackey et al. (2017); Michalka et al. (2015); Wang et al. (2015).
Function	Top-down vs bottom-up spatial attention	The FEF and IFJ are both involved in top-down attention, and show evidence of sustained activity in response to a cue. However, IFJ activity profile is more context-dependent, and influenced by bottom-up factors as well. The role of the IFJ could be of modulating DAN activity according to the current task demands, and of toggling between DAN and VAN activity.	Asplund et al. (2010); Corbetta and Shulman (2002); Marshall et al. (2015); Ruff et al. (2006); Tamber-Rosenau et al. (2018); Vossel et al. (2012); Wen et al. (2012); Zanto et al. (2011).
Function	Spatial vs non-spatial attention and spatial vs object working memory	The FEF is predominantly involved in processing spatial information, mediating the set of overlapping functions of covert spatial attention, oculomotor control, and spatial working memory. In contrast, recent studies using MVPA revealed that the IFJ is involved in processing non-spatial information (i.e., in feature- and object-based attention and working memory tasks). The analysis of effective connectivity has also allowed to identify the IFJ as the source of modulation of feature-based attention and working memory encoding signals.	Baldauf and Desimone (2014); Gong and Liu (2020); Jerde et al. (2012); Liu (2016); Liu et al. (2011); Nee and D'Esposito (2016); Sneve et al. (2013); Zanto et al. (2010); Zhang et al. (2018).
Function	Multiple demand system (inclusion in the multiple demand system)	Several studies have now reported that the IFJ (and in particular, the IFJp) belongs to the core multiple demand system. There are also indications that the IFJa and FEF may display partial multiple demand characteristics, although this possibility needs to be further researched.	Assem et al. (2020); Duncan (2010); Fedorenko et al. (2013); Muhle-Karbe et al. (2017); Noyce et al. (2017).
Connectivity	Connectivity fingerprints (structural connectivity, resting-state functional connectivity, meta-analytic connectivity modeling)	The FEF is reached by the terminations of the SLF1 and SLF2. In contrast, we speculate that the IFJ may be reached by the terminations of the SLF2 and SLF3, thus suggesting partially segregated anatomical pathways from the pPFC to posterior parietal and temporo-parietal cortices. The FEF is one of the core regions of the DAN, while the IFJ is part of the frontoparietal network. Meta-analytic connectivity modeling reveals three main co-activation patterns in the left IFJ, including a pattern related to attentional control.	Cieslik et al. (2016); Cole and Schneider (2007); De Pasquale et al. (2010); de Schotten et al. (2011); Fox et al. (2006); Ji et al. (2019); Ngo et al. (2019); Parlatini et al. (2017); Sundermann and Pfeleiderer (2012); Vincent et al. (2008); Yeo et al. (2011).

In this work, we have purposefully emphasized a perspective on functional specialization in the PFC that focuses on the representational format (spatial vs. non-spatial) and that was pioneered thanks to the comparative studies by Goldman-Rakic and colleagues (Goldman-Rakic, 1996; Romanski, 2004; Scallidhe et al., 1997, 1999; Wilson et al., 1993). Although we think that this is one of the most valuable frameworks to understand the organization of the pPFC, there are several other principles of organization of the PFC that are worth taking into account. Among these, the level of abstraction and the difficulty level of

the task performed are the two most important factors that are usually invoked to explain gradients in its organization, typically along the rostro-caudal axis (Koechlin et al., 2003; Nee & D’Esposito, 2016; O’Reilly, 2010). We would like therefore to conclude this review by presenting several open questions that are in our opinion the most urgent and intriguing to further disentangle which are the peculiar contributions of the FEF and IFJ to goal-driven behaviour and particularly to top-down attention and working memory (Table 3).

Table 3 Open questions and future directions

1	Based on connectivity fingerprint matching, which region is more likely to be the homolog of the human IFJ in the macaque?
2	Are the FEF and IFJ reliably tied to predefined sulcal landmarks at the individual subject level? What is the role of inter-individual differences in sulcal organization in localizing these regions?
3	Does the IFJ encode information at a more abstract level compared to the FEF? Within the IFJ, are there different levels of abstraction encoded in distinct sub-populations, or is there a gradient of increasing abstraction from the posterior to the anterior IFJ?
4	Are the structural connectivity fingerprints of the FEF and IFJ indicative of a segregation in their afferent and efferent connections with the dorsal and the ventral visual streams?
5	Similarly, are these connectivity fingerprints recapitulated in resting-state fMRI and MEG activity? Can these be used to fractionate the attention (i.e., the DAN and VAN) and frontoparietal networks according to the representational content encoded (spatial vs non-spatial)?
6	Can we causally demonstrate a dissociation between the role of the FEF and IFJ in the control of spatial vs non-spatial attention using TMS?

Given that many sources of evidence of a dissociation between the selectivity to spatial, as opposed to feature and object information, in the plPFC are comparative (Bichot et al., 2015, 2019; Constantinidis & Qi, 2018; Goldman-Rakic, 1996; Riley et al., 2017; Wilson et al., 1993), we would like to discuss some of the most noteworthy proposals of quantitative approaches establishing homologies in the plPFC in humans and macaques. In this regard, several challenges ought to be addressed. First, the lack of similar sulcal organization in macaques and the relative expansion in the size of the human PFC (Donahue et al., 2018) complicate any solution that relies on the purely geometrical inter-species registration of these areas. Second, even though cytoarchitecture may serve as a guiding principle in identifying homologies, in the PFC, it is usually at best a coarse approximation, for example, as illustrated by the fact that FEF lies in different BAs in the macaque and the human (viz., BA8 and BA6, and BA6, respectively; Paus, 1996; Petit & Pouget, 2019; Tehovnik et al., 2000). This implies that the cytoarchitecture of the PFC in the macaque isn’t necessarily a good predictor of the location where fMRI activity is usually measured using conventional FEF localizer tasks in humans (for instance, see fig. 2C from Amiez et al., 2006). The third challenge is methodological: in humans, the cortical organization is usually inferred non-invasively with MRI, whereas invasive methods are still the most widely adopted to study non-human primates. As a particularly glaring example, consider the definition of structural connectivity in macaques and humans: the first inferred from tracing studies on small populations of animals, but with a negligible number of false positives, whereas the

latter is inferred non-invasively from large populations, but where current tractography algorithms are only partially able to reproduce the former results (Donahue et al., 2016; van den Heuvel et al., 2015). Also, the latter do not yet offer a convenient solution to the filtering of large amounts of false positives (Maier-Hein et al., 2017). We review below some recent proposals that may allow overcoming these limitations. The problem of registering cortical maps between species (i.e., from the macaque to the human, and vice versa) has been recently addressed by employing advanced registration algorithms (i.e., multimodal surface matching; Robinson et al., 2014) that can simultaneously rely on multiple cortical features. Although the specific approach adopted in comparative studies may differ in relation to the research question addressed, and in particular in the way structural (e.g., myelin content; Eichert et al., 2020) as opposed to functional information (e.g., gradients; Xu et al., 2020) is exploited to drive the registration, this framework represents a promising solution to cross-species mapping. In parallel to these advancements, the field of primate neuroimaging is witnessing a rapid acceleration in the development of MRI data acquisition protocols, analysis pipelines and data sharing (Autio et al., 2020; Hayashi et al., 2021; Milham et al., 2018). These developments will likely lead to the creation of a macaque multimodal parcellation from a large cohort of animals, comparable with last decade's research trends in humans (e.g., Glasser et al., 2016; Yeo et al., 2011), derived from the combination of invasive and non-invasive methods. This will allow researchers to propose an updated cortical taxonomy in this species, and this may in turn allow the precise mapping of homotopic brain regions between macaques and humans (Van Essen et al., 2019).

In two highly influential implementations of comparative neuroimaging, Sallet et al. (2013) and Neubert et al. (2014) used dMRI data to perform a k-means clustering based on structural connectivity (as inferred from probabilistic tractography) to parcel the dorsal and the ventral human PFC, respectively. They then computed the functional connectivity from resting-state fMRI data in humans (from the previous parcellation) and macaques (based on an existing cytoarchitectonic atlas) to compare the connectivity fingerprints of each area between the species. They showed that the similarity of these connectivity fingerprints, as measured by the functional coupling scores, allowed them to quantitatively identify homologies in the PFC across these species. In their studies, the human 'FEF-like' cluster corresponded to area 8A in the macaque (denoted cluster 8/8A; Sallet et al., 2013), and the IFJ to area 44 in the macaque (Neubert et al., 2014). In an additional analysis using an ROI that merged the 8A cluster from the study by Sallet et al. (2013) with the IFJ, Neubert et al. (2014) performed an additional connectivity-based parcellation and confirmed that their IFJ parcel was distinct from the former in all the subjects analysed ($n = 25$). However, a limitation of these studies is that they used already established homologies between the macaque and the human brain to identify the target regions and compute the connectivity fingerprints of their seeds in PFC. Furthermore, in the macaque, all these regions (both seeds and targets) were based on cytoarchitectonic definitions (Neubert et al., 2014; Sallet et al., 2013). It is unclear at present how well these criteria represent functionally meaningful subdivisions of the PFC and if these are adequate to establish such homologies.

An extremely interesting development of this connectionist framework posits that the most appropriate method for establishing homologies should be grounded on the cross-species alignment of white-matter bundles (Mars, Sotiropoulos, et al., 2018). If we indeed assume that certain white-matter bundles are preserved across species, the connectivity blueprints of the vertices localized near their terminations (which essentially are matrices that describe the connectivity of these vertices on the grey-matter surface with each bundle) can allow us to disentangle between the alternative interpretations of areal expansion in size (if they relate to these bundles in a similar fashion), their relocation across the cortical sheet or their connectional reorganization relative to the last common ancestor (if they are highly dissimilar). In addition to its intuitive appeal, because most of these bundles have been identified (Mars, Sotiropoulos, et al., 2018, refer to 39 bundles as homologues), and their segmentation using dMRI has been already validated for most of them using *ex vivo* data in both species, this proposal is undoubtedly one of the most promising avenues for macro-anatomical alignment of functional areas. Using these connectivity blueprints, Mars, Sotiropoulos, et al. (2018) were able to predict the localization of MT+ in the macaque from human hMT+ and, conversely, to predict the localization of the pre-supplementary motor area in humans from macaque F6, using dMRI data acquired in both species. Concerning the specific problem of identifying FEF and IFJ homologies across primates, it would be therefore interesting to address the following questions (see the first question in Table 3): Do the human connectivity fingerprints and connectivity blueprints of these areas match well with those found in the macaque PFC? If so, which region is the homologue of the human IFJ in the macaque (see Bichot et al., 2015, 2019, and Figure 1 for potential correspondences)? Are any differences explained by the connectivity reorganization in the plPFC, the relocation of its areas, or are they consistent with their expansion in size? Finally, is there any evidence that the SLF, one of the major frontoparietal bundles, has similar cortical terminations in the human and other primates (de Schotten et al., 2011; Hecht et al., 2015)? Answering these questions will enable us to better position the divergence of FEF and IFJ functions along primates' evolutionary path, as well as to perform inferences motivated by comparative evidence on humans in a more reliable way.

A question that is strongly intertwined with the former is whether at present our knowledge of the localization of the FEF and IFJ in standard space (i.e., Talairach and MNI152 space) can be considered reasonably accurate and robust in terms of inter-individual differences in the sulcal organization (see question two in Table 3). As we have argued in Section 2.2.2, the FEF and IFJ seem to be tied in a very reliable way to specific sulcal landmarks of the plPFC, although evidence from fMRI analyses performed at the single-subject level is to date quite limited (Amiez et al., 2006; Derrfuss et al., 2009, 2012; Kastner et al., 2007). In Glasser et al. (2016; see figs 7 and 8 in the 'Supplementary Results and Discussion'), the authors reported that in 24 subjects out of 210, area 55b (ventrally adjacent to the FEF) had an atypical organization. In nine of these subjects, its localization was shifted dorsally, and in 12 other subjects, this area was split so that the FEF joined its border with the ventral premotor eye field, hence also possibly affecting the average localization of these neighbouring regions. A worrying consequence of this potential spatial uncertainty is that it would severely limit the conclusions reached by any study of brain

connectivity (whether based on structural, functional or both information) that did not identify the FEF and IFJ using separate fMRI localizers. In Tables 4 and 5, we have listed the standard coordinates of the FEF and IFJ from the studies discussed in this review. As shown in these tables, the variability in the average localization of the FEF and IFJ seems quite remarkable, particularly along the sagittal plane in the case of the FEF (see Table 4). This may not only be due to genuine inter-individual variability in the sulcal organization (in addition to the variability in the acquisition sequence, MRI scanner and the often-large smoothing factor adopted in most fMRI analysis pipelines) but also to the idiosyncratic experimental tasks, contrasts and analytic procedures that were adopted in these fMRI studies to localize the FEF and IFJ. An intermediate solution, in the cases in which running an fMRI localizer is not a viable option, would be to rely on the results of meta-analytic methods, such as the ALE technique (Eickhoff et al., 2012). Even though this technique should be able to approximate well the typical localization of the FEF and IFJ, we suggest that to infer the most accurate localization of the functionally defined FEF and IFJ in standard space, one would need to additionally define a gold standard for FEF and IFJ fMRI localizer tasks to better refine the study inclusion criteria. In the case of the FEF, we would imagine that reaching a consensus would not be too difficult, as the involvement of this area in oculomotor control has been studied extensively (Paus, 1996; Petit & Pouget, 2019; Vernet et al., 2014). In contrast, due to the involvement of the IFJ in several and potentially non-overlapping cognitive functions (Ngo et al., 2019; Sundermann & Pfeiderer, 2012), an effort of specifying a set of core processes to consistently localize this region in both hemispheres would be needed, which at present seems challenging (but see Derrfuss et al., 2005, for a relevant suggestion).

Turning to the functional roles of the human FEF and IFJ, we have reported converging evidence from fMRI and M/EEG studies that the first is predominantly involved in coding spatial information, whereas the second is predominantly involved in coding non-spatial information (feature and object information). While MVPA approaches have generally reported evidence supporting this claim (Jerde et al., 2012; Liu, 2016; Liu et al., 2011; Meyyappan et al., 2021; Muhle-Karbe et al., 2017), we suggest that experimental manipulations that allow keeping sensory stimulation identical during the delay period but employ different cues (spatial vs. non-spatial) can be effectively used to evaluate our current proposal within a single experimental design and in a variety of behavioural paradigms (e.g., see Meyyappan et al., 2021). We would like to stress that one could even push this logic further and suggest that if decoding analyses were to show an above-chance performance when a classifier is trained on FEF activity when non-spatial cues are presented in a purely feature- and object-based paradigm (but not when trained on IFJ activity), and vice versa, an above-chance performance when a classifier is trained on IFJ activity when spatial cues are presented (but not when trained on FEF activity), this would severely challenge our hypothesis regarding the functional specialization of the FEF and IFJ.

Table 4 List of the group-level coordinates of FEF in standard space from the studies discussed in this review

Study	N	Age	Method / Paradigm	Studies / Contrast	Space	Hemisphere	Coordinates		
							x	y	z
Amiez et al. (2006) *	8	28; 22-42	Functional localizer	Prosaccade > Fixation	MNI	L	-38	-9.8	54.4
						R	34.5	-10.8	52.5
Anderson et al. (2012) *	10	29 ± 3	Functional localizer	Voluntary saccades in darkness > Fixation	MNI (SPM2)	L	-60	4	38
						R	52	-6	46
Cieslik et al. (2016)	12 experiments	Healthy adults	ALE fMRI meta-analysis	Prosaccade > Rest & Prosaccade > Fixation (conjunction analysis)	MNI	L	-40	-2	50
						R	44	4	50
De Pasquale et al. (2010)	10	29 ± 6	Literature review	Sources: He et al. (2007), Shulman et al. (1997)	MNI	L	-26.3	-11.8	52.7
						R	30.3	-12.8	52.6
Kastner et al. (2007) *	4	20-36	Functional localizer	Prosaccade > Fixation	Talairach	L	-35	-12	49
						R	36	-9	50
Koyama et al. (2004) *	20	N. A.	Functional localizer	Prosaccade > Fixation	MNI (SPM99)	L	-26	-12	54
						R	18	-6	56
Meysenppan et al. (2020)	20	N. A.	Endogenous cueing paradigm	Spatial and feature-based task cue-evoked activity	MNI	L	-27	-1	52
						R	36	2	49
Mitchaka et al. (2015)	10	27.1; 22-31	Cued RSVP	Attend visual > Attend auditory	MNI (Freesurfer)	L	-33	-7	47
						R	34	-6	48
Nee and D'Esposito (2016)	23	19.9; 18-28	Executive control paradigm	Main effects of temporal and contextual control and their interaction with feature control	MNI	L	-24	4	54
						R	31	-2	47
Paus (1996)	60	N. A.	PET meta-analysis	Oculomotor tasks	Talairach	L	-32	-2	46
						R	31	-2	47
Ruff et al. (2006) *	4	29-35	Functional localizer	Voluntary saccades in darkness > Rest	MNI (SPM2)	R	33	1	62
Thamer-Roseman et al. (2018) *	10 (8 L, 10 R)	28.5 ± 3.3	Functional localizer	Prosaccade > Fixation	Talairach	L	-23.5	-9.88	45.75
						R	25.1	-9.8	45.2
Umarova et al. (2010) *	26	30 ± 7.3	Functional localizer	Attend blocks > Fixation	MNI (SPM5)	R	51	3	48
Vossel et al. (2012) *	24	26.83; 20-37	Functional localizer	Valid trials > Baseline	MNI single subject	L	-28.7	-6.3	50.8
						R	34.6	-1.9	50.8
Wen et al. (2012) *	12	20-28	Functional localizer	Attend > Passive-view	MNI (SPM2)	L	-30	-3	54
						R	30	0	57
Yeo et al. (2011)	7 studies	N. A.	Meta-analysis	Saccadic eye-movements	MNI	L	-26	-6	48
Zhang et al. (2018)	19	19-26	Feature-based attention paradigm	All voxels activated by the stimulus block	Talairach	R	-42	-5	35
						R	40	-5	39
Average coordinates *	7 studies (n = 86) 9 studies (n = 118)		All functional localizers	Covert attention / Prosaccades > Fixation	MNI	L	-34.6 ± 12.31 35.71 ± 10.77	-5.42 ± 6.28 -2.96 ± 4.85	50.24 ± 6.99 53.19 ± 5.55

Table 5 List of the group-level coordinates of IFJ in standard space from the studies discussed in this review

Study	N	Age	Method / Paradigm	Studies / Contrast	Space	Hemisphere	Coordinates			
							x	y	z	
Asplund et al. (2010) *	30	N.A.	RSVP paradigm	Surprise trials > Search trials	Talairach	L	-40	8	25	
						R	37	5	29	
Balduf and Desimone (2014) *	12	23-37	Object-based attention paradigm	Attend face & Attend house blocks > Passive view	MNI (SPM8)	L	-38	11	30	
						R	47	9	31	
Cole and Schneider (2007) *	9	19-42	Working memory paradigm	Target switching trials target non-occluded > Non-switching trials target non-occluded	Talairach	L	-46	2	36	
						R	42	8	31	
Derrfuss et al. (2005)	14 Switching & 11 Stroop studies	N.A.	ALE fMRI meta-analysis	Task-Switching, Set-Shifting, and S-R Reversal studies	Talairach	L	-40	4	30	
				Color-word Stroop studies		L	-40	4	32	
Derrfuss et al. (2009) *	14 (13 R)	24 ± 1.9	Task-switching paradigm	Meaning-switch trials > Cue-switch trials	Talairach	L	-39	2	32	
						R	42	2	31	
Derrfuss et al. (2012) *	12	25.3 ± 2.4; 22-31	Stroop paradigm	Incongruent trials > Congruent trials	MNI	L	-42	6	33	
Han and Marois (2014) *	14	20-32	RSVP / Oddball paradigm	Target trials > Distractor trials	Talairach	L	-45	3	22	
						R	44	5	26	
Meyyappan et al. (2020) *	20	Undergraduates	Endogenous cuing paradigm	Spatial and feature-based task cue-evoked activity	MNI	L	-42	11	25	
						R	42	11	25	
Muller-Kaabe et al. (2014)	45 Task-switching studies (n = 817)	N.A.	ALE fMRI meta-analysis	Switch trials > Repetition trials	MNI	L	-40	4	32	
Muller-Kaabe et al. (2017)	23	24.09 ± 5.06	ALE fMRI meta-analysis	Based on Derrfuss et al. (2005)	MNI (SPM8)	L	-40	4	30	
						R	44	10	34	
Nee and D'Esposito (2016) *	23	19.9; 18-28	Executive control paradigm	Main effect of temporal and contextual control and their interaction with feature control	MNI	L	-40	10	20	
				Anatomical definition & Main effect of all visual stimuli		L	-44	3	33	
Sneve et al. (2013) *	6	21-28	Working memory paradigm		MNI	R	45	1	35	
Sundermann and Plederer (2012)	11F; 180 experiments (n = 2,274)	N.A.	MACM fMRI meta-analysis	Cuebird seeds adapted from the coordinates reported in Brass et al. (2005)	Talairach	L	-47	5	34	
						R	47	5	34	
Tamler-Rosenau et al. (2018) *	10 (8 L, 9 R)	28.5 ± 3.3	Functional localizer	Presaccades > Fixation	Talairach	L	-37.75	2.88	24.75	
						R	40.67	1.22	25	
Zanto et al. (2010) *	13	25; 20-31	Working memory paradigm (n-back)	Functional connectivity attend color/motion vs. ignore color/motion	MNI	L	-48	4	26	
						R	42	0	26	
Zanto et al. (2011) *	20	24.25; 18-31	Working memory paradigm (n-back)	Functional connectivity attend color/motion vs. ignore color/motion	MNI	L	-56	8	36	
						R	44	20	24	
Zhang et al. (2018) *	21	19-26	Feature-based attention paradigm	Stimulus block effects	Talairach	L	-42	9	31	
						R	44	11	29	
Average coordinates *	13 studies (n = 202)		All paradigms	Covert and overt attention, working memory and cognitive control studies	MNI	L	-43.78 ± 4.88	7.80 ± 3.18	28.30 ± 5.59	
	11 studies (n = 167)					R	44.96 ± 2.55	8.94 ± 5.92	27.21 ± 3.63	

Another critical issue for evaluating the current proposal is to determine how exactly this information is coded by these regions at the computational level. In the working memory literature, an influential family of models emphasizes a distinction between regions that encode working memory information from other regions that dynamically exert control over these stored representations, possibly localized in the parietal and frontal cortices (reviewed in Serences, 2016; Sreenivasan et al., 2014). In the instance of the FEF and IFJ, are these regions only involved in the executive components of working memory, with the information being encoded at the distributed network level? If this isn't the case, at which level of abstraction are the sensory representations situated so they can guide attentional selection and influence working memory performance? We have reviewed studies that, thanks to the use of MVPA, have been able to decode attended and remembered information from both the FEF (Jerde et al., 2012) and the IFJ (Liu, 2016; Liu et al., 2011). This suggests that activity in these regions during the delay period doesn't merely reflect a control signal over other brain regions but actually contains some ongoing information processing related to the cue/memoranda itself. However, at present, it is unclear whether the FEF and IFJ encode this information at the same level of abstraction. Although both areas are positioned near the output layer of the cognitive system, based on the involvement of the IFJ in encoding stimulus-response mappings according to novel task rules (Muhle-Karbe et al., 2017), and in a variety of other high-level cognitive operations (Assem et al., 2020; Brass et al., 2005), it could be argued that the IFJ may encode information at a higher level of abstraction compared with the FEF (reviewed in Section 2.3.3). This would be consistent with the relatively recent emergence of the IFJ along the evolutionary path of the primate species compared with the more ancient dorsal pathway's regions (Caminiti et al., 2015; Mars, Sotiropoulos, et al., 2018). We therefore suggest that this hypothesis should be investigated more systematically in future studies (see question three in Table 3). For example, one could design an n-back fMRI experiment requiring either the encoding of the abstract identity of an object or its viewpoint and apply MVPA to the FEF and IFJ to see whether the decoding accuracy differs between the two in these tasks. We suggest that because the 'identity' task is more independent of low-level visual features compared with the 'viewpoint' task, we should expect a better decoding accuracy within the IFJ compared with the FEF (see the study by Henderson & Serences, 2019, for interesting results that are in line with these predictions).

The PFC is generally characterized by a high degree of interconnectedness between its areas and with the rest of the brain—a property that is thought to underlie its unique contribution to complex behaviour (Fuster, 2001; Yeterian et al., 2012). This information aids to delineate the organization of the PFC along two principal axes: a rostro-caudal (Koechlin et al., 2003) and a dorsoventral axis (Goldman-Rakic, 1996). According to the results of the study by Nee and D'Esposito (2016), it is the mid-lateral PFC that is positioned at the apex of the PFC hierarchy, based on the asymmetries in its effective connectivity patterns. In their model, the FEF and IFJ show sensitivity to the stimulus context and sensory domain (spatial vs. verbal) and are hence hypothesized to be under the control of the cMFG and IFS, respectively (Nee & D'Esposito, 2016). In an updated version of this hierarchical model of cognitive control, Badre and Nee (2018) place the FEF and IFJ in the sensory-motor control areas that allow the maintenance of goal-related information to control movement in a

domain-specific way; thus, although they are embedded in different information processing streams, they seem to be localized within the same gradient of the rostro-caudal axis. The authors also hypothesize that lateral areas could be similarly influenced by motivational factors that are propagated from the dorsomedial PFC at a comparable gradient in the PFC hierarchy (Badre & Nee, 2018). This suggestion parallels developments from the last decade in cognitive models of attention, which began to incorporate distinct forms of attentional biases stemming from learning processes and motivational factors (Anderson, 2019; Awh et al., 2012; Macaluso & Doricchi, 2013). It is however still unknown how these signals shape activity in the PFC (a possibility that we suggest should be investigated in future studies), and how the FEF and IFJ dynamically interact with subcortical and thalamic structures to achieve efficient control of behaviour (Halassa & Kastner, 2017; White et al., 2017).

Finally, we would like to highlight some of the most promising future research directions that would allow dissociating the function of the FEF and IFJ. As we have argued throughout this review, the concept of connectivity fingerprints (Mars, Passingham, & Jbabdi, 2018; Passingham et al., 2002) provides a useful framework to tackle this problem. If we assume that the FEF and IFJ occupy a dissociable functional role in the brain networks underlying visual attention, visual working memory and cognitive control, this leads to the prediction that this differentiation could be reflected in their connectivity fingerprints. If we build upon the difference of the representational format they encode, this contrast might allow for the individuation of a spatial and a non-spatial network based on their structural and functional connectivity with parietal, temporal and early visual cortices (see questions four and five in Table 3). More specifically, this hypothesis would entail predominant structural and functional connectivity with topographic visual areas (Wang et al., 2015) from the FEF, and vice versa, predominant structural and functional connectivity of the IFJ with areas that are involved in central vision, coding for visual feature and object representations (Kravitz et al., 2013). Another interesting hypothesis would be to investigate whether the parietal cortex contains regions to which the associative fibres from the plPFC send segregated projections, as well as regions in which they converge, therefore possibly enabling the communication between these two processing streams, as it would be predicted, for example, by neural models of priority maps (Fecteau & Munoz, 2006; Zelinsky & Bisley, 2015). As we mentioned in Section 2.4.1, the limited evidence on the structural connectivity patterns of the FEF, which is even more pronounced in the case of the IFJ, is quite astonishing given the increasing number of publications that investigated these regions. Nevertheless, the existent data make both these hypotheses plausible, and their likelihood is further strengthened in the light of comparative evidence (Caminiti et al., 2015; Croxson et al., 2005; de Schotten et al., 2011; Felleman & Van Essen, 1991; Kravitz et al., 2013; Yeterian et al., 2012).

In contrast, studies on resting-state fMRI allowed gathering an impressive amount of information about the involvement of the FEF and IFJ in specific brain networks (Ji et al., 2019; Yeo et al., 2011). Despite their power to encapsulate functional activity at the whole-brain level, it is still unknown how well these networks offer a good model for the co-activation patterns that are measured using experimental manipulations in task fMRI (however, see Tavor et al., 2016). In particular, in the case of the FEF and IFJ, their

assignment to these network parcellations likely represents a convenient way to operate a dimensionality reduction on their activity patterns (and their hypothesized functions), but at the cost of losing track of their multiple and varied co-activation patterns. Therefore, we suggest that techniques such as MACM (Robinson et al., 2010; reviewed in Section 2.4.3) should be regarded as the most relevant source of evidence when attempting to dissociate the FEF and IFJ based on their functional connectivity patterns.

Top-down selection and working memory maintenance typically involve a complex chain of neural activity patterns, and this dynamic nature cannot be underestimated. Tracking the temporal profile of this activity at an appropriate timescale is therefore crucial to understand selective visual behaviour (Fiebelkorn & Kastner, 2019). Due to the limited temporal resolution, fMRI is not suited to resolve the complete role of the FEF and IFJ at different stages of information processing, the transient versus sustained nature of their activity and the interplay of spectral activity within the attention networks. Another outstanding issue pertains to the role of rhythmic activity in specific frequency bands, which is a distinctive signature of many perceptual, attentional and working memory processes (Buschman & Miller, 2007, 2009; Fiebelkorn & Kastner, 2019; Fries, 2005; VanRullen, 2016). Electrophysiological methods (M/EEG, electrocorticography) should be able to close this gap by providing accurate measures of FEF and IFJ activity as it unfolds over time (Baldauf & Desimone, 2014; Chacko et al., 2018; Martin et al., 2019; Michalareas et al., 2016; Popov et al., 2017; Szczepanski et al., 2014; Tabarelli et al., 2020). Furthermore, the analysis of functional and effective connectivity metrics should allow modelling the reciprocal links between FEF and IFJ activities. As representative examples of this approach, the studies by Sneve et al. (2013), Baldauf and Desimone (2014) and Zhang et al. (2018) contributed in a foundational way to show that functional and effective connectivity metrics can be used to identify the sources of the attentional biases observed in feature- and object-based attention and in working memory tasks. More specifically, their studies together suggest that the IFJ may be responsible for modulating activity elsewhere to support non-spatial selection and working memory encoding. The role of the FEF is in contrast to that of a spatial priority map (Fecteau & Munoz, 2006; Itti & Koch, 2001; Thompson & Bichot, 2005), which likely binds non-spatial and spatial information and maps it to an overt response. The careful combination of these analytical techniques will likely lead in the future to uncover how task information is transferred between the FEF and IFJ and posterior regions. Concerning this question, recently, it has been proposed that informational connectivity could be used to investigate directed information transfer between brain regions (Anzellotti & Coutanche, 2018) by modelling how well activity patterns in a brain region can help to predict activity in another region. This multivariate technique preserves the information contained in all the voxels, overcoming the issues associated with univariate approaches (i.e., averaging), hence being optimally adept to uncover mechanisms that are not apparent even with the application of MVPA to single brain regions. Another great advantage of this technique is that the experimental conditions/stimuli classes can be carefully chosen to determine which information content is driving the informational connectivity between specific regions (Anzellotti & Coutanche, 2018), which we suggest is a feature that can be

clearly leveraged to investigate our hypothesis of spatial and non-spatial control from the FEF and IFJ to posterior regions.

Finally, arguably one of the most direct ways to dissociate the contributions of the FEF and IFJ to selective visual behaviour would be to perform a TMS experiment using an endogenous cueing paradigm alternating spatial and feature-based attention blocks (see question six in Table 3). During the delay period, the experimenter would administer repetitive pulses of TMS to the FEF and the IFJ in each block and assess their effects on behavior. Our main prediction would be to observe a dissociation in the effects of the stimulation that is specific to each region and which interacts with the type of cue presented within a block (e.g., spatial vs. colour cue). Because most of the studies reviewed above point towards the right lateralization of the attention networks, the proposed study could initially focus on stimulating the FEF and IFJ in the right hemisphere.

Visual attention and working memory play a fundamental role in our increasingly cluttered and distracting environments. Understanding the neural mechanisms and the brain networks underlying these functions is crucial for cognitive neuroscience, but it is ultimately also a relevant goal for clinical and industrial applications that could greatly benefit from this basic knowledge. By contrasting the structure, function and connectivity fingerprints of the FEF and IFJ, we have provided some insights into how comparative research and multimodal neuroimaging data can be fruitfully combined to study the organization of the plPFC and to dissociate the function and connectivity fingerprints of the FEF and IFJ as we continue to investigate the neural mechanisms of selective goal-driven behaviour.

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AUTHOR CONTRIBUTIONS MB conceptualized the organization of the review, collected the references, wrote the initial draft and prepared the figures and tables. DB supervised the writing of the manuscript and the preparation of the figures and tables, revised them and suggested additional references. Both authors contributed to the general discussion by proposing avenues for future research. Finally, they both revised and agreed on the final version of the manuscript.

Chapter 3

Accurate localization and coactivation profiles of the frontal eye field and inferior frontal junction: an ALE and MACM fMRI meta-analysis

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3.1 | INTRODUCTION

Owing to the capabilities that likely derive from the massive expansion in the cortical surface allowed by the folding patterns of the cortex (Van Essen 2007; Welker 1990; Zilles et al. 2013), which particularly involved the prefrontal and association cortices (Donahue et al. 2018; Toro et al. 2008), humans possess one of the most complex behavioral repertoires in nature (Mesulam 1998; Miller and Cohen 2001). A fundamental aspect of functional specialization in the human brain is its relationship with cortical neuroanatomy (Van Essen 2007). Microstructural features pertaining to cortical architecture (i.e., cyto- and myelo-architecture), such as cell types and layer organization, are a major determinant of the functional organization of the brain, and they provide important information about regional segregation (Brodmann 1909; Amunts et al. 2020). Over the past 30 years, magnetic resonance imaging (MRI; and in particular, functional MRI) became the dominant technique for investigating this organization non-invasively and *in vivo* (Eickhoff et al. 2018). Although regional delineations inferred based on architectonic criteria (e.g., cytoarchitecture) generally agree well with information gathered from MRI/fMRI (Amunts and Zilles 2015), such correspondences should be always interpreted with caution. These criteria may be weak predictors of functional organization in highly heterogeneous regions, for example when regions sit at the boundary of different Brodmann areas (BA; Brodmann 1909). Moreover, this relationship may be affected by strong inter-individual differences, which were not taken into account in most of the previous invasive studies characterized by relatively small sample sizes (Amunts and Zilles 2015). In addition to the previous prevalent invasive and lesion-based approaches, another way of conceptualizing functional organization and, more in general, the relationship between cognitive processes and their neural substrate, emerged from fMRI research with the functional localization approach (Kanwisher 2010). Specialized computations are performed by brain regions that can be reliably identified across individuals with fMRI using standard tasks (thus usually referred to as functional localizers; Kanwisher et al. 1997; Kanwisher 2010; O'Craven et al. 1999; Peelen and Downing 2005). In combination with the functional localization approach, research on structural MRI has shown that, despite the remarkable inter-individual variability in the organization of the gyri and sulci across the whole cortex (Desikan et al. 2006; Destrieux et al. 2010; Ono et al. 1990; Petrides 2018), these functional modules can also be localized based on anatomical landmarks (Fischl et al. 2008), which suggests a developmental link between the functional differentiation of brain regions and the mechanisms of cortical maturation (Zilles et al. 2013).

In sum, in the human brain, functional specialization appears to be tightly linked and possibly follows from brain structure, although it remains to be established exactly to what degree this principle holds within specific systems. In the prefrontal cortex (PFC), two structures, the frontal eye field (FEF) and the inferior frontal junction (IFJ) have largely overlapping but complementary roles, being involved in several orchestrating functions such as attention, working memory, cognitive control, and other top-down processes (Baldauf and Desimone 2014; Bedini and Baldauf 2021). In our previous review, we have in particular argued that despite these overlaps, it is their patterns of neural selectivity to spatial (FEF) vs non-spatial information (IFJ) that allows the dissociation of their role across these different

functions (Bedini and Baldauf 2021). This functional specialization may in turn provide an effective way to localize these regions with fMRI. While the FEF has been studied extensively both in human and non-human primates, its precise localization and relationship to sulcal morphology in humans, and correspondence to the macaque FEF has proven to be difficult to establish (Amiez and Petrides, 2009; Petit and Pouget 2019; Schall et al. 2020; Tehovnik et al. 2000; but see Koyama et al. 2004). Evidence also suggests that FEF localization may be affected by substantial individual differences (Amiez et al. 2006; Kastner et al. 2007; Paus 1996; see Bedini and Baldauf 2021, for a discussion of this issue in the context of the multimodal parcellation (MMP1) by Glasser et al. (2016). The prevailing view is that the human FEF lies in the ventral bank of the superior precentral sulcus (sPCS), near its junction with the superior frontal sulcus (SFS; see Paus 1996 and Vernet et al. 2014, for a meta-analysis and a review of FEF localization, respectively). However, some authors have argued that instead, a region localized ventrally in the dorsal branch of the inferior PCS (iPCS), termed the inferior FEF (iFEF, or sometimes the lateral FEF) may be the putative homolog of the macaque FEF (Kastner et al. 2007; Schall et al. 2020). Moreover, it has been raised the related question of whether the inferior FEF has been under-reported in the fMRI literature (Derrfuss et al. 2012). In topographic mapping studies, peaks corresponding to the iFEF have been already reported (Kastner et al. 2007; Mackey et al. 2017) albeit they were not as consistent as FEF peaks in their presence across subjects and relative localization. Moreover, at least one study has previously reported activations in the iFEF using a saccadic localizer task, which were clearly segregated from those elicited by a Stroop task (Derrfuss et al. 2012). These analyses were performed in native space on an individual-subject basis, which is a very powerful approach that allows for carefully studying dissociations in adjacent neuroanatomical regions (Fedorenko 2021). The IFJ, a region found ventrally and anteriorly relative to the iFEF, is typically localized near the junction of the iPCS with the inferior frontal sulcus (IFS), sometimes encroaching into its caudal bank (Derrfuss et al. 2005). The IFJ was only much more recently characterized as a separate brain region (based on structural; Amunts et al. 2006; and functional criteria; Brass et al. 2005) that performs both specialized (Baldauf and Desimone, 2014; Bedini and Baldauf 2021) and general domain computations (Assem et al. 2020; Derrfuss et al. 2005), in line with the multiple demand hypothesis (Duncan 2010). Currently, however, due to the interspersed and close arrangement of specialized and multiple demand regions near the IFJ, common activation foci resulting from various cognitive processes have not been reported yet across experiments (see however Assem et al. 2020, for evidence from high-resolution fMRI data and improved inter-subject alignment methods).

Clearly, there is a need to better characterize the relationship between anatomy and functional specialization within the PFC. This is particularly critical, as the large inter-individual variability in the organization of the prefrontal areas and sulci (Germann et al. 2005; Juch et al. 2005) complicates the interpretation of the results of previous studies and may partly explain the discrepancies in the findings reported across research groups and methods. That such a link can in principle be successfully accomplished has been demonstrated in the visual system, where studies have shown that despite the inter-individual variability in the overall size, shape and position of the early visual cortex, specific

anatomical landmarks (i.e., sulci) coincide very well with the borders of primary visual areas as derived from various sources of data, including cytoarchitecture, retinotopic mapping, myelin content and resting-state fMRI functional connectivity (Abdollahi et al. 2014; Fischl et al. 2008; Glasser et al. 2016; Sereno et al. 1995). For example, in Hinds et al. (2008) the authors used surface-based registration methods (Fischl et al. 1999) to identify V1 in new subjects from cortical folding information (i.e., the stria of Gennari) and showed that these methods outperformed volumetric methods in labeling this structure (see also Hinds et al. 2009). Similarly, Benson et al. (2012) used folding information to predict visual responses within the striate cortex to a retinotopic mapping fMRI protocol. When moving up into the cortical visual hierarchy, however, the relationships between cortical folding and other neuroanatomical information become more difficult to establish and interpret (Coalson et al. 2018; Glasser et al. 2016). Wang et al. (2015) created a probabilistic atlas of 25 topographic visual areas and showed that anatomical variability (as measured by the variance in gyral-sulcal convexity across subjects) and the overlap of functional activations (measured as peak probability values) were negatively correlated, particularly in higher-order visual areas, suggesting that the former may play an important role in shaping functional organization. Similarly, in one of the most comprehensive efforts to parcel the cortical surface with high-resolution non-invasive methods, Glasser et al. (2016) found that the lateral PFC is one of the brain districts where the intrinsic neuroanatomical variability is higher than in the rest of the brain (Glasser et al. 2016; Juch et al. 2005), as measured by a decrease in the test-retest reliability of their parcellation. While the former limitations (i.e., the weaker association between cortical folding and function, and inter-individual variability, which particularly affects volumetric group-level analyses; Coalson et al. 2018) have posed significant challenges to the interpretation of the relationship between cortical folding and functional specialization in higher-order visual regions, several studies have shown that adopting an individual-level approach in defining sulci may bear important implications for understanding cognitive function within the PFC (Amiez et al. 2006; Amiez and Petrides 2018; Derrfuss et al. 2009; Fedorenko 2021; Miller et al. 2021). For example, the study by Frost and Goebel (2012) showed that, by leveraging the former approach and improving the alignment in the cortical folding patterns (hence limiting the influence of the anatomical variability across subjects) using a technique termed curvature-driven cortex-based alignment, the overlap in FEF localization increased by 66.7% in the left hemisphere and 106.5% in the right hemisphere compared to volume-based registration in a sample of 10 subjects. These results suggest that the FEF is indeed strongly bound to a macro-anatomical location (i.e., the junction of the sPCS and the SFS; Paus 1996), and more generally the presence of a strong structure-to-function relationship in this region (see also Wang et al. 2015). In the study by Derrfuss et al. (2009), which again was carried out using an individual-level approach, 13 out of 14 subjects showed activations localized between the caudal bank of the IFS and the iPCS that corresponded to the anatomical description of the IFJ in a task-switching paradigm. Taken together, these studies point to the need to better characterize the relationship between sulcal morphology and functional specialization within the PFC. This research line may in the future allow predicting functional activity from neuroanatomical information alone, thus accomplishing one of the fundamental goals of contemporary cognitive neuroscience in terms of inferring structure-to-function relationships (Felleman and Van Essen 1991; Osher et al.

2016; Passingham et al. 2002; Saygin et al. 2012; Young et al. 2000). In summary, the organization of the regions localized along the banks of the major sulci of the posterior-lateral PFC (plPFC), namely the SFS, the sPCS, the iPCS, and the IFS, has yet to be clarified spatially.

In this study, we aimed to accurately localize the FEF and IFJ based on standard fMRI localizer tasks. These are well-validated tasks designed to target pre-defined ROIs (Fedorenko 2021; Kanwisher 2010) and are typically performed independently from the main fMRI task. In particular, we wanted to reassess the precise localization of the FEF and its relationship with the localization of the iFEF as inferred using saccadic localizer tasks in the light of recent fMRI evidence (see Grosbras et al. 2005, Jamadar et al. 2013, and Paus 1996, for previous meta-analyses using fMRI and PET experiments). Further, we also wanted to re-examine the precise localization of the IFJ by inferring the convergence of activations across paradigms (Derrfuss et al. 2005; Muhle-Karbe et al. 2016). This information may provide important clues for better-interpreting activations in the posterior-lateral PFC based on combined structural and functional criteria. Coordinate-based meta-analyses offer a convenient way to summarize and model the uncertainty in the activations found across several PET/fMRI experiments (Fox et al. 2014) based on specific paradigms and contrasts of interest, overcoming inter-individual variability, and allow to establish adequately powered brain-behavior relationships. Here we employed the activation likelihood estimation (ALE) technique (Eickhoff et al. 2009, 2012) to accurately infer the localization of the FEF and IFJ activation peaks in standard space. By using the inferred ALE peak coordinates as seeds, we also performed a meta-analytic connectivity modeling (MACM) analysis (Langner and Camilleri 2021; Robinson et al. 2010) to investigate the coactivation profiles of FEF and IFJ in fMRI studies across paradigms in a data-driven fashion. Overall, our study goal is to offer some consensus and anatomical priors to localize these regions with fMRI, and to guide future non-invasive brain stimulation studies. In addition, our study also aims to provide the meta-analytic groundwork to investigate the relationship between the functional specialization and connectivity of the FEF and IFJ in large multimodal neuroimaging datasets (e.g., the Human Connectome Project; Van Essen et al. 2013).

3.2 | MATERIALS AND METHODS

3.2.1 | Activation likelihood estimation fMRI meta-analysis method

The ALE is a powerful meta-analytic technique that allows for assessing the spatial convergence of the activations reported in the neuroimaging literature (Eickhoff et al. 2009, 2012). As a coordinate-based technique, ALE takes as input the activation peaks reported by several independent neuroimaging studies and tests their significance against a null distribution of the foci across the whole brain (Eickhoff et al. 2012). This ALE feature is particularly useful given that in the neuroimaging literature results are usually reported and summarized as x, y, z coordinates in standard space (Talairach or MNI), rather than as full activation maps accompanied by a statistical summary of the effect sizes, and even more rarely shared in that form (for important initiatives in neuroimaging data sharing see however

NeuroVault: <https://neurovault.org/>, Gorgolewski et al. 2015; OpenNeuro: <https://openneuro.org/>, Markiewicz et al. 2021; BALSA: <https://balsa.wustl.edu/>, Van Essen et al. 2017, and Anima: <https://anima.inm7.de/index.php>, Reid et al. 2015, among other initiatives). This aspect becomes crucial in the case of brain regions that may be under-reported in the fMRI literature (such as the iFEF; Derrfuss et al. 2012; Kastner et al. 2007) or which only recently began to be included in the brain atlases taxonomy (such as the IFJ; Bedini and Baldauf 2021; Sundermann and Pfleiderer 2012). Here, we exploited this ALE feature by applying this technique to analyze two independent collections of fMRI studies performed over the last 30 years with the primary aim of accurately inferring FEF and IFJ localization in MNI152 space using the GingerALE software (v. 3.0.2; <https://www.brainmap.org/ale/>). In the ALE procedure, each set of foci reported in a study is modeled as a three-dimensional Gaussian distribution centered around the coordinates and whose size is determined based on the experiment sample size (Eickhoff et al. 2012). In particular, larger sample sizes result in tighter Gaussians, which reflects lower uncertainty about the ‘true’ location reported, whereas lower samples lead to larger Gaussians that are more spread around the respective peak coordinates, thus conveniently reflecting lower confidence about their corresponding locations. These activations are then combined into a modeled activation map for each experiment of a study. Importantly, in the revised ALE algorithm, within-study effects that could result from the summation of adjacent foci are minimized, so that studies that reported activation in a higher number or more densely organized foci won’t drive the ALE results disproportionately (Turkeltaub et al. 2012). By computing the union of all these modeled activation maps, an ALE score for each voxel in the brain is obtained (Eickhoff et al. 2009, 2012). The significance of these scores is then assessed by comparing them with the null distribution obtained by randomly reassigning the modeled activations across the whole brain with a permutation approach. Finally, the thresholded p-values are usually corrected for multiple comparisons using either voxel-level or cluster-level family-wise error (FWE). The use of uncorrected p-values and false discovery rate is instead generally not advised since it can lead to spurious findings (Eickhoff et al. 2016).

The present meta-analysis focused on specific cognitive functions (described more in detail in the ‘Study selection criteria’) in which the FEF and IFJ and the associated brain networks are relatively well-known to be involved. More specifically, in what we will refer to in the following as the ‘FEF sample’, we applied the ALE technique to several independent fMRI studies requiring the planning and execution of visually-guided and voluntary eye movements, as a considerable number of previous studies clearly showed that these types of tasks elicit activation in the FEF, and other eye fields (for previous meta-analyses see Cieslik et al. 2016; Grosbras et al. 2005; Jamadar et al. 2013; Paus 1996). In particular, tasks requiring the execution of prosaccades and antisaccades contrasted against a fixation baseline are the most prevalent and consensually established FEF functional localizer in the human fMRI literature (Amiez et al. 2006; Amiez and Petrides 2018; Kastner et al. 2007). In the case of the ‘IFJ sample’, it is arguably more difficult to pinpoint a universally accepted functional localizer for this region, and in fact, very few studies have implemented a separate and targeted localizer paradigm to isolate the IFJ (for relevant examples see Baldauf and

Desimone 2014; Zanto et al. 2010; Zhang et al. 2018) for subsequent analyses. In addition, there is increasing evidence that the IFJ may be characterized as a region more generally involved in different and often overlapping functions (i.e., a multiple demand region; Assem et al. 2020; Derrfuss et al. 2005; Sundermann and Pfeleiderer 2012), which may even further complicate the definition of a standard localization method. Therefore, in the ‘IFJ sample,’ we anticipate that we analyzed data from a more heterogeneous collection of fMRI studies investigating covert attention, working memory, and cognitive control across a wider range of paradigms. Whenever the sample sizes of the studies retrieved allowed for it, we also carried out post hoc control analyses to examine potential spatial discrepancies between the IFJ peaks derived from splitting up the full localizer sample according to specific cognitive functions and paradigms (see Supplementary Information p. 5 and 14-15).

3.2.2 | Study selection criteria

The selection criteria of the sample of studies for the present meta-analysis followed the best-practice recommendations and guidelines by Müller et al. (2018). Multiple bibliographic searches were performed between May 2019 and January 2021 (cutoff date). A final search was conducted with the same criteria and cutoff dates (i.e., 1st of January 1990 - 1st of January 2021) by the first author MB to comply with the updated PRISMA guidelines (Page et al. 2021) and as a sanity check. The selection procedure is reported in Figures S1 and S2 (created based on the PRISMA flow diagram; Page et al. 2021), which refer to the ‘FEF sample’ and the ‘IFJ sample’, respectively. All the bibliographical searches were carried out using Web of Science (<https://www.webofscience.com>). We searched records in the Web of Science Core Collection using the keywords ‘fMRI’ AND ‘frontal eye field’ (all fields) in the first instance, and ‘fMRI’ AND ‘inferior frontal junction’ (all fields) in the second. We complemented these results with other sources (Google Scholar, personal collection of articles and references cited by the studies retrieved) by one of the authors (MB). In the FEF sample, our search identified a total of 711 records, from which we removed all the review papers. 665 records were further screened, and 470 of these were sought for retrieval to assess their adequacy with respect to the inclusion criteria (described below). In the IFJ sample, 375 results were identified, from which, after removing review papers, 356 records were further screened, and 142 of these were sought for retrieval to assess their adequacy with respect to our original inclusion criteria. The general inclusion criteria consisted of the following. Each study selected: 1. Reported coordinates in standard space (either MNI or Talairach); 2. Was an fMRI study (we decided to not include positron emission tomography studies as our goal was to keep our samples as homogeneous as possible in terms of the signal measured, the spatial resolution and analysis pipelines (Botvinik-Nezer et al. 2020) to make our results specific to the fMRI field); 3. Performed on a scanner of 3T or higher field; 4. Tested and reported results from healthy adults (18-60 years old; or an appropriate control group in the case of clinical studies); 5. The study acquired whole-brain fMRI data or with a FOV that was sufficiently large to cover the frontal cortex and in particular its posterior aspect (see the Supplementary Tables 1 and 2 for the FOV of each study). Even though the latter criterion would lead to the inclusion of studies with partial brain coverage, which is generally not recommended in ALE analyses (Müller et al. 2018), given that our main

research question focused on the standard localization of the FEF and IFJ, we motivate it by accepting the tradeoff derived from having access to a larger sample for these regions, as opposed to having less sensitivity in detecting other regions that are consistently active during the tasks included (which however are not the main focus of the present study), but not reported simply due to the lack of brain coverage. In the Supplementary Information, we report the results of a control analysis excluding first studies with partial brain coverage and second, studies performing ROI analyses, as per the best practices recommended by Müller et al. (2018). The last group of inclusion criteria is specific to each sample (the FEF or the IFJ) and is primarily related to the type of experimental paradigm utilized in the fMRI study and the specific contrasts analyzed (described more in detail below). Here, we strived to find a balance that would adequately represent the various localization methods that have been pursued in the fMRI literature, while also assigning a higher weight in the sample to the more standardized and replicated localization approaches.

3.2.3 | FEF sample inclusion criteria

The human FEF is a well-characterized region in the fMRI literature (Bedini and Baldauf 2021), although some uncertainties persist regarding the correspondence of its localization obtained from fMRI compared with other methods (i.e., brain stimulation; Vernet et al. 2014) and with the macaque FEF (Koyama et al. 2004; Petit and Pouget 2019). The region is crucially involved in the top-down control of eye movements and spatial attention (Astafiev et al. 2003; Beauchamp et al. 2001; Corbetta et al. 1998), and it is considered a prominent node of the dorsal attention network (Corbetta and Shulman 2002; De Pasquale et al. 2010; Fox et al. 2006; Yeo et al. 2011). A very simple and time-efficient yet effective way to localize the FEF in fMRI scans is to have participants perform an experimental block of visually-guided saccades towards an unpredictable peripheral target, and contrast this activation with a fixation block (Amiez and Petrides 2006). The resulting activations - usually found near the junction of the SFS and the sPCS - are then assumed to correspond to the FEF (Paus 1996). However, depending on the statistical thresholds and analytical approach adopted, in addition to this superior cluster, often this type of contrast reveals a more widespread pattern of activity along the banks of the iPCS (Beauchamp et al. 2001; Kastner et al. 2007). Therefore, this localization method doesn't seem to have adequate functional specificity if not combined with the additional anatomical criteria mentioned above. Building on this approach, the antisaccade task and its neural mechanisms have been extensively studied in the primate neurophysiology literature (Munoz and Everling 2004), and this task has been employed as a measure of inhibitory control in healthy and clinical populations in humans (Hutton and Ettinger 2006). Briefly, in the antisaccade task, the subject is required to keep fixation until a visual target appears and to look at its mirror location (Hallet 1978). Computationally, this requires at least two mechanisms: the first one inhibits a reflexive saccade towards the visual onset, and the second is responsible for executing a saccade towards the opposite location (the endpoint is in this case endogenously generated; Munoz and Everling 2004). An interesting feature of this task is that compared to the prosaccade task, it gives rise to frequent direction errors, which reflect a failure to inhibit reflexive behavior (Hutton and Ettinger 2006; Munoz and Everling 2004; Pierrot-Deselleigny et al.

2002). Inserting a short (e.g., 200 ms) gap period before the presentation of the target decreases saccadic reaction times (Saslow 1967) and further increases the ratio of these direction errors (Munoz and Everling 2004). fMRI studies comparing the regions involved in prosaccade vs antisaccade task performance have found overlapping activations in the FEF in both tasks, although the antisaccade task recruits additional regions that seem to reflect the increased executive demands of this task (McDowell et al. 2008). Within FEF, there is also increased activity in the antisaccade compared to the prosaccade task (Connolly et al. 2000). This is particularly evident during the preparatory phase (Brown et al. 2006; Connolly et al. 2002; Curtis and Connolly 2008; DeSouza et al. 2003; Ford et al. 2005) and when the two tasks are presented in a mixed fashion (Pierce and McDowell 2015, 2017). Based on these results, it could be hypothesized that contrasting antisaccades vs prosaccades may offer better specificity to localize clusters of activity within the FEF compared to the prosaccade vs fixation blocked design described earlier. Previous studies didn't address this hypothesis directly, and it still needs to be tested in a within-subject design by comparing the activation topographies at the individual subject level. Finally, in modified versions of the spatial cueing paradigm (Fan et al. 2005; Posner 1980), univariate analyses contrasting valid vs neutral/invalid trials are often used to localize all the main regions belonging to the dorsal attention network (Corbetta and Shulman 2002), which are subsequently used as ROIs for functional and effective connectivity analyses (for example, see Vossel et al. 2012, and Wen et al. 2012). It can be argued that, even though these adaptations are not generally employed as independent functional localizers for the FEF, they may be well adept to isolate this region under the assumption that covert and overt shifts of spatial attention have a shared and overlapping source in this region, which seems well supported by fMRI (Astafiev et al. 2003; Beauchamp et al. 2001; Corbetta et al. 1998; Jerde et al. 2012) and comparative evidence (Buschman and Miller 2009; Moore and Fallah 2001; reviewed in Fiebelkorn and Kastner 2020). Indeed, the studies that directly investigated this question generally reported a strong degree of spatial overlap, although they also suggest that the signal measured in covert paradigms tends to be weaker than in overt tasks (Beauchamp et al. 2001; De Haan et al. 2008) and thus possibly less robust across fMRI data analysis pipelines (Botvinik-Nezer et al. 2020). Thus, an open question is whether oculomotor and covert spatial attention tasks are equally efficient in localizing the FEF.

In summary, for the reasons introduced above, we included in the FEF sample all the studies that investigated the planning and execution of visually-guided and voluntary eye movements (prosaccades and antisaccades) as well as covert spatial attention using both blocked and event-related designs, analyzing mainly the following contrasts: 1. prosaccades > fixation; 2. antisaccades > fixation; 3. prosaccades & antisaccades > fixation; 4. anti-saccades > pro-saccades; 5. valid > neutral/invalid trials (see Figure S1 for an overview of the selection procedure following the PRISMA2020 guidelines; Page et al. 2021; for the full list of studies and the related information see Tables S1 and S2 in the Supplementary Information). Combining these contrasts allowed us to carry out our main analysis complemented by three control analyses, respectively designed to replicate a previous study (Cieslik et al. 2016) and to investigate two additional research questions (see Supplementary Information p. 4). In our main localizer analysis, we pooled together all studies that reported

at least a contrast related to the planning and execution of prosaccades, both prosaccades and antisaccades, and antisaccades, contrasted with a fixation baseline.

3.2.4 | IFJ sample inclusion criteria

In contrast to the FEF, the IFJ doesn't have a broadly accepted homolog in the macaque (Bedini and Baldauf 2021; see however Bichot et al. 2015, 2019; and Neubert et al. 2014) and its role started to be investigated only much more recently with fMRI (Brass et al. 2005). Its functional profile remains to date not well understood and is characterized by a remarkable functional heterogeneity (Muhle-Karbe et al. 2016; Ngo et al. 2019). Consistent with this idea, recent high-resolution fMRI studies showed that the IFJ (and in particular, the posterior IFJ as defined according to the MMP1 by Glasser et al. 2016) belongs to the core multiple-demand system of the brain (Assem et al. 2020, 2021), which identifies a set of regions that are engaged in multiple processes often across different cognitive domains (Duncan 2010). This particular position in the cognitive processing architecture arguably poses a severe challenge in trying to define a gold standard for an fMRI localization method for this region, which would allow for effectively segregating it from adjacent coactive regions (for an excellent example of such an approach see however Derrfuss et al. 2012; we return to this point in the discussion). Several promising approaches to localize the IFJ both at the individual and at the group level have nevertheless previously been reported from different research groups ranging from attention and working memory to cognitive control paradigms. For example, the series of studies from the group led by Brass and colleagues were critical in establishing the IFJ as a region involved in task preparation and more generally in cognitive control (Brass and Von Cramon, 2002, 2004; Derrfuss et al. 2004; see also Cole and Schneider 2007).

In summary, based on the evidence discussed above, in the IFJ sample, we decided to include attentional (i.e., rapid serial visual presentation (RSVP) and endogenous cueing paradigms), working memory (primarily n-back paradigms), and cognitive control paradigms (i.e., task-switching and Stroop tasks). These inclusion criteria were based on Derrfuss et al. (2005), who investigated switching and Stroop paradigms, and we extended them to attentional and working memory paradigms that presumably also tap cognitive control functions. These paradigms all stress the maintenance of a task set to control behavior, which should be one of the integrative IFJ functions according to our hypothesis. The main contrasts analyzed were therefore quite heterogeneous, but can be broadly grouped into the following primary ones (see Figure S2 for an overview of the selection procedure following the PRISMA2020 guidelines; Page et al. 2021; for the full list of studies and the related information see Table S2): 1. Oddball > Target trials in covert attention paradigms (e.g., RSVP paradigms); 2. Functional connectivity with a seed perceptual region (e.g., V4, V5, FFA) in the Attend > Ignore condition in n-back paradigms; 3. Switching > Repetition trials in task-switching paradigms; 4. Incongruent > Congruent trials in Stroop paradigms (see the Supplementary Information for control and contrast analyses).

In conclusion, the final sample of the included papers for our ALE meta-analysis was $n = 51$ for the FEF, and $n = 30$ for the IFJ sample (see the Supplementary Information, Figures S1 and S2, and Tables S1 and S2 for a summary of the studies). The number of experiments was 35 for the FEF localizer sample, and 32 for the IFJ localizer sample. Both sample sizes were within the recommended range (i.e., a minimum of 17-20 experiments) to have adequate statistical power with ALE as derived from empirical simulations (Eickhoff et al. 2016).

3.2.5 | Activation likelihood estimation procedure

We extracted all the foci from the studies included in the FEF and IFJ samples, and we converted all the Talairach coordinates to the MNI152 space using the Lancaster transform as implemented by the function provided in the GingerALE software (v. 3.0.2; Laird et al. 2010; Lancaster et al. 2007). We note that after the SPM2 version, the MNI templates distributed are consistent across FSL and SPM software packages, being compliant with the ICBM-152 coordinate space (Fonov et al. 2009), so for any later version of these packages we used the Talairach to MNI FSL transform. Where other software packages were used for spatial normalization, we again employed the Talairach to MNI FSL transform for consistency, as the other transformation provided in GingerALE represents a pooled FSL/SPM transformation (Lancaster et al. 2007) that would only lead to systematic displacement of the coordinates. In only two cases (i.e., Manoach et al. 2007; Mao et al. 2007) the studies employed the mapping from MNI to Talairach developed by Brett et al. (2002). These coordinates were therefore mapped back to the MNI space using this specific transformation, as recommended in the GingerALE user manual.

For the main localizer analyses (FEF and IFJ localizer samples), the ALE parameters were set to 10000 threshold permutations (as recommended in Eickhoff et al. 2016) and a voxel-level FWE of 0.01 was applied (Eickhoff et al. 2017) with a minimum cluster size of 50mm^3 (corresponding to 6 voxels). Compared to cluster-level FWE inference, which can only allow inferring that a given cluster is above a significance threshold as a whole, but critically, not that any putative region that is included in the cluster is individually significant on its own (Eickhoff et al. 2016), voxel-level FWE allows to more readily interpret all the cluster extent as well as its peak location from the main localizer samples anatomically (Eickhoff et al. 2016). Moreover, our sample sizes ensured that these clusters would not be driven by a contribution exceeding 50% of any individual study. Therefore we would like to stress that performing the ALE procedure for the main localizer samples using voxel-level FWE arguably represents the most conservative approach to inferring spatial convergence in our samples and allows us to interpret individual voxel ALE values as a proxy for the most active location across experiments. When retrieving the relevant foci, we first grouped the studies by subject group rather than by experiment (Turkeltaub et al. 2012). This was done because grouping by subject group further minimizes within-study effects (Turkeltaub et al. 2012). When a single experiment reported multiple contrasts of interest, we therefore pooled them under the same subject group. We note that however, in all cases in which the studies reported more than one contrast of interest they were drawn from the same experiment (with

very few exceptions; see Tables S1 and S2), so our strategy didn't unfairly pool together partially independent observations and was practically almost equivalent to grouping by experiment. When an experiment failed to report significant activation for some ROIs, we used the lower number of subjects that had above threshold activations in all ROIs from a contrast of interest if this information was available. In summary, our study grouping strategy allowed us to fully exploit the information gathered from the different contrasts that were performed in the original studies and also to carry out our control analyses with the largest possible sample sizes. To validate the results of the main ALE analyses and to further assess the reliability of the ALE peaks found, we also carried out a leave-one-experiment-out procedure (LOEO; Eickhoff et al. 2016) on the main FEF and IFJ localizer samples using the same foci grouping strategy. Since we found identical ALE peaks as in the main ALE analyses using 1000 threshold permutations, we performed the LOEO procedure with the same parameter to reduce computational times.

3.2.6 | Comparison method of the ALE clusters and peaks with previous coordinate-based meta-analyses, relationship to macro-anatomical information and the MMP1

To interpret our results more carefully, we compared the significant activation clusters from our ALE main localizer analyses with the results from previous meta-analyses results and brain atlases (Derrfuss et al. 2005; Glasser et al. 2016; Klein et al. 2012; Paus 1996). First, we described the anatomical location of each cluster and assigned the corresponding Brodmann label using the Talairach Daemon in GingerALE (Lancaster et al. 2000). Second, to compare our results with previous meta-analyses (Derrfuss et al. 2005; Paus 1996), we mapped our ALE peaks to the Talairach space using the transformation developed by Lancaster et al. (2007) as implemented in GingerALE (MNI (FSL) to Talairach; see Table 3). Third, to relate our results to surface-based atlases (Klein et al. 2012; Glasser et al. 2016), we followed two distinct approaches. The Mindboggle 101 atlas (Klein et al. 2012) describes the macro-anatomical organization of the human brain as delineated by sulcal and gyral information. The atlas was recently mapped to the MNI152 non-linear symmetric template (Manera et al. 2020), so we manually imported this atlas in FSL and in FSLeaves as described in this GitHub repository: [The-Mindboggle-101-atlas-in-FSL](https://github.com/brain-map-lab/mindboggle-101-atlas-in-fsl). We assigned one of the Mindboggle 101 labels to each of the ALE peak coordinates using the atlasquery command-line tool with FSL (v. 6.0.3; Jenkinson et al. 2012). For atlases that were released and best interpreted in a surface-based format, such as the MMP1 (Glasser et al. 2016; see Coalson et al. 2018 for an in-depth discussion), we instead employed the mapping technique developed in Wu et al. (2017) to register our ALE results from the MNI152 space (Fonov et al. 2009) to FSaverage (Fischl et al. 1999). A version of the MMP1 (Glasser et al. 2016) mapped to the FSaverage surface was made available using the method described in Mills (2016; https://figshare.com/articles/dataset/HCP-MMP1_0_projected_on_fsaverage/3498446). Once we mapped the ALE clusters to this surface, we also mapped the MNI152 coordinates corresponding to each ALE peak to a vertex on the inflated surface (Wu et al. 2017) and we assigned each of these to the respective MMP1 labels (Table 5). To describe the anatomical

labels associated with each ALE cluster using more specific labels (compared to the Talairach Daemon), we used a volumetric version of this atlas for convenience. The source files that were used to import the atlas are the same as in Huang et al. (2021). The volumetric version of the MMP1 was manually imported in FSLeyes as described in this GitHub repository: [The-HCP-MMP1.0-atlas-in-FSL](#)).

3.2.7 | Meta-analytic connectivity modeling method

After obtaining the ALE peaks from the main localizer analyses, we exploited this information to perform a data-driven analysis of the coactivation patterns of the FEF and the IFJ across the whole brain to uncover their task-based fMRI functional connectivity fingerprint (Langner and Camilleri 2021; Passingham and Wise 2002). We therefore retrieved all the papers matching specific criteria (described below) from the BrainMap database using Sleuth (<https://www.brainmap.org/sleuth/>; Fox and Lancaster 2002), and we analyzed these foci by employing the MACM technique (Robinson et al. 2010). This technique leverages the ALE algorithm and allows inferring all the regions that coactivate with a given seed region that is selected a priori. This analysis also allowed us to perform a reverse inference on these coactivation patterns (Poldrack 2011). More specifically, we sought to functionally decode and characterize the various behavioral domains that are associated above chance with each of these by using a standardized taxonomy (Fox et al. 2005) via the Mango software (v. 4.1) behavioral analysis plugin (v. 3.1; Lancaster et al. 2012).

The studies were retrieved from the BrainMap database using Sleuth according to the following fields (all linked using the ‘AND’ operator) and specifications: in the Experiment field, the “context” field was set to “normal mapping”, in the “activation” field we searched for “activations only”, with “Imaging modality” being set to “fMRI”. Finally, four separate searches were conducted in the BrainMap database by setting the “locations” field as corresponding to each left hemisphere (LH) and right hemisphere (RH) seed region (LH FEF, RH FEF, LH IFJ, and RH IFJ). We first transformed each seed location from MNI152 to Talairach space (which is the standard in Sleuth and also used internally by Mango’s behavioral plugin) using the transformation by Lancaster et al. (2007; the FSL transformation) and we created cuboid seeds of 6 mm centered around the respective ALE peaks. With these criteria, we were able to retrieve a range of 19 to 53 studies across seed locations. In particular, we retrieved 26 studies (27 experiments) for the LH FEF seed, 19 studies (19 experiments) for the RH FEF seed, 53 studies (59 experiments) for the LH IFJ, and 31 studies (31 experiments) for the RH IFJ. We note that the different number of studies retrieved possibly reflects a combination of the increased base probability of finding activations within a specific ROI (Langner et al. 2014) but also the fact that some ROIs tend to participate in multiple functional networks (Langner and Camilleri 2021). Thus, while our sample size was generally greater in the case of the IFJ, this information matches what was previously reported about the coactivation patterns of FEF and IFJ (the IFJ being part of the frontoparietal network, that has been previously shown to work as a hub network; Cole et al. 2013). More importantly, these sample sizes allowed for adequately powered inference using ALE (Eickhoff et al. 2016). Therefore, we used all the foci retrieved separately from each seed location as inputs for GingerALE. The ALE parameters were set to an 0.001 uncorrected

p-value, 1000 threshold permutations and a cluster-level FWE of $p < 0.01$. In the functional decoding analysis, we used the same 6 mm cuboid seeds as in the MACM analysis centered around the respective FEF and IFJ ALE peaks. Associations with behavioral domains were considered statistically significant when their z-score was ≥ 3 , corresponding to a threshold of $p < 0.05$ (Bonferroni corrected).

3.3 | RESULTS

3.3.1 | FEF and IFJ localizer samples ALE main clusters

In the FEF localizer sample, the activations converged most strongly in two main clusters localized in the left and right posterior dorsolateral PFC. Two ALE peaks were found near the junction of the sPCS with the SFS, localized in the anterior (in the LH) and posterior (in the RH) banks of the sPCS (Figure 1). These peaks match well the classical description of the human FEF as inferred with fMRI (Petit and Pouget 2019; Vernet et al. 2014). Our LOEO procedure overall confirms the reliability of the localization of these ALE peaks (see Table 3; LH: 26/35; RH: 23/35). In the IFJ localizer sample, the activations converged more strongly in two main clusters localized in the left and right posterior ventrolateral PFC. These clusters extended both in the dorsal and ventral portion of the iPCS, partially encroaching on the IFS (see Figure 1). The cluster in the right hemisphere was slightly more focused spatially compared to the cluster in the left hemisphere. Crucially, in both clusters, we found that the ALE peaks were localized along the posterior bank of the iPCS, near its ventral junction with the IFS, which closely matches the description of the IFJ (Derrfuss et al. 2005; Muhle-Karbe et al. 2016). Again, our LOEO procedure overall suggests that these ALE peaks are highly reliable across experiments (see Table 3; LH: 31/32; RH: 24/32).

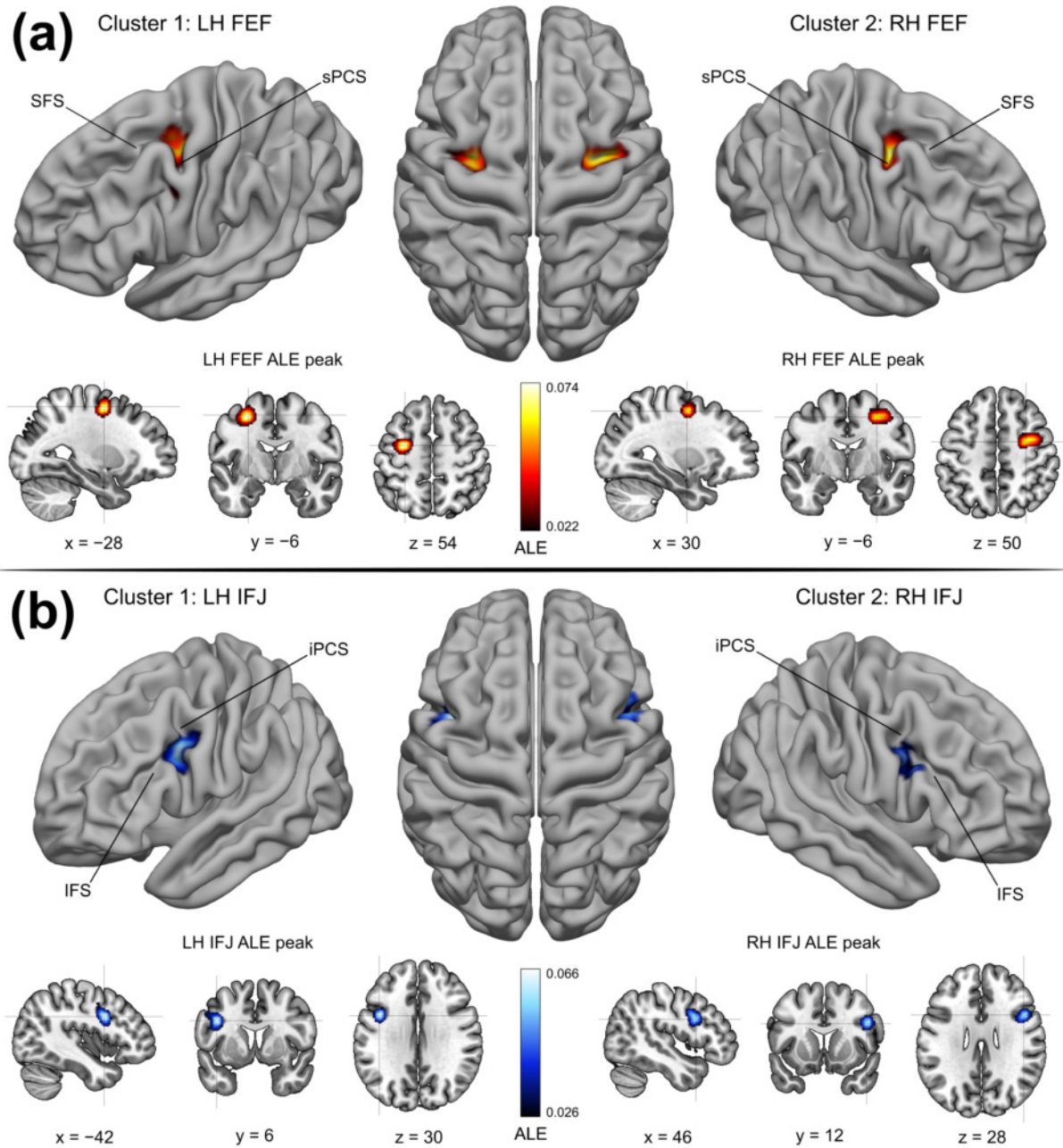


FIGURE 1 FEF and IFJ localizer samples - ALE main clusters. **A** ALE results from the FEF localizer sample. Two main clusters were found in the posterior dorsolateral PFC, which corresponds to the description of the anatomical location of the FEF (Paus 1996; Vernet et al. 2014). The FEF peaks were localized at the junction of the sPCS and the SFS, in the anterior (in the LH) and posterior (in the RH) banks of the sPCS. **B** ALE results from the IFJ localizer sample. Two main clusters were found in the posterior ventrolateral PFC, and their respective peaks were localized along the posterior bank of the iPCS, near its ventral junction with the IFS. The location of these peaks and the corresponding MNI coordinates match the description of the IFJ (Derrfuss et al. 2005; Muhle-Karbe et al. 2016)

3.3.2 | FEF localizer sample ALE results - FEF lateral peak and other significant clusters

In the left hemisphere, we also found a lateral peak within the main FEF cluster, which was localized on the bank of the iPCS, dorsal to its junction with the IFS (see Figure 2). This lateral peak corresponds to what has been previously referred to as the inferior or the lateral FEF (Derrfuss et al. 2012; Kastner et al. 2007; Luna et al. 1998). In addition to the main FEF clusters in the left/right PFC, the ALE technique revealed three other consistently activated clusters. These clusters were localized in the medial frontal gyrus and the left/right posterior parietal cortex (Table 1). The cluster in the medial frontal gyrus comprised the SCEF (Amiez and Petrides 2009) and the dorsal cingulate motor cortex (Glasser et al. 2016). In the posterior parietal cortex, two bilateral superior clusters spanned the precuneus and the SPL (Scheperjans et al. 2008a, 2008b), and an additional cluster was found in the right anterior intraparietal area (Glasser et al. 2016; Numssen et al. 2021).

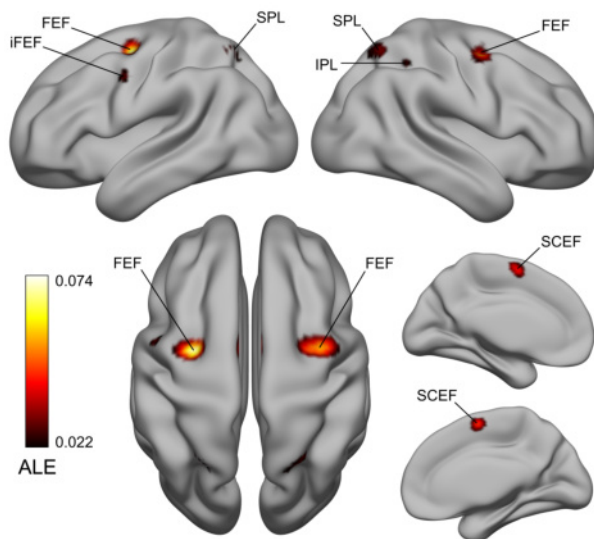


FIGURE 2 FEF localizer sample ALE results - FEF lateral peak and other significant clusters. In the FEF localizer analysis, we also found a lateral peak in the LH, which was localized near the bank of the iPCS, dorsal to its junction with the IFS, corresponding to the iFEF (Kastner et al. 2007; Luna et al. 1998). It is unclear whether this region should be considered part of the FEF proper (Glasser et al. 2016; Mackey et al. 2017). We found three other significant clusters localized in the supplementary and cingulate eye field (SCEF) and the dorsal cingulate motor cortex, and the precuneus/superior parietal lobule (SPL) and

the right anterior intraparietal area

Table 1 FEF localizer sample ALE results

Cluster	Macroanatomical location	Hemi	MNI152 coordinates			ALE value	Volume (mm ³)	BA
			x	y	z			
1	Precentral Gyrus	L	-28	-6	54	0.0736	4784	6
	Precentral Gyrus	L	-48	-2	40	0.0293		6
2	Precentral Gyrus	R	30	-6	50	0.0623	4208	6
3	Medial Frontal Gyrus	L/R	0	0	58	0.0547	3016	6
4	Precuneus	L	-22	-58	56	0.0418	1512	7
5	Precuneus	R	24	-60	56	0.0376	1056	7
6	Inferior Parietal Lobule	R	36	-46	48	0.0262	168	40

3.3.3 | IFJ localizer sample ALE results - Other significant clusters

In addition to the main IFJ clusters in the left/right PFC, we found seven consistently activated clusters forming a broad fronto-parietal network (see Figure 3). In the frontal cortex, the first cluster was localized in the in the dorsal anterior cingulate cortex (dACC; Cole and Schneider 2007) and SCEF (Amiez and Petrides 2009), a second in the left precentral gyrus (within the putative FEF), and finally, two other clusters were localized in the bilateral insular cortex and claustrum (Table 2). Posteriorly, we also found a cluster in the left SPL/inferior parietal lobule (IPL), and a smaller cluster in the right SPL/IPL (Numssen et al. 2021; Scheperjans et al. 2008a, 2008b).

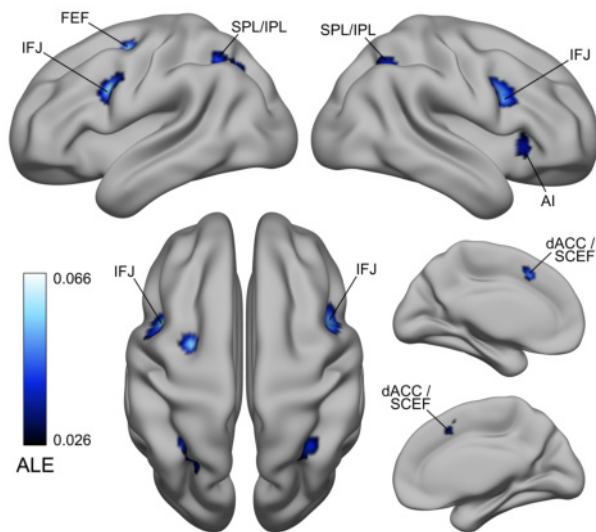


FIGURE 3 IFJ localizer sample ALE results - Other significant clusters. In addition to the bilateral IFJ clusters, we found significant activations in the dACC/SCEF, the left FEF, in two clusters in the insular cortex and claustrum (not visible in the left hemisphere), and finally, in the SPL/IPL. Given that these areas were activated across different paradigms, we suggest that they could be associated with the “encoding and updating of task-relevant representations” as first hypothesized by Derrfuss et al. (2005). From a network perspective, they belong to the frontoparietal

network (Cole et al. 2013; Yeo et al. 2011)

Table 2 IFJ localizer sample ALE results

Cluster	Macroanatomical location	Hemi	MNI152 coordinates			ALE value	Volume (mm ³)	BA
			x	y	z			
1	Precentral Gyrus	L	-42	6	30	0.0657	3488	6
2	Inferior Frontal Gyrus	R	46	12	28	0.0597	3016	9
3	Medial Frontal Gyrus	L	-2	18	44	0.0573	2328	6
4	Superior Parietal Lobule	L	-30	-54	48	0.0444	1504	7
	Precuneus	L	-26	-66	44	0.0388		7
5	Precentral Gyrus	L	-28	-4	54	0.0577	1208	6
6	Superior Parietal Lobule	R	34	-56	48	0.0408	800	7
7	Clastrum	R	32	22	-2	0.0385	728	*
8	Clastrum	L	-30	18	2	0.0342	424	*

3.3.4 | Spatial relationship of the main FEF and IFJ clusters and ALE peaks with previous coordinate-based meta-analyses, macro-anatomical information and the MMP1

The comparison of the FEF and IFJ ALE peaks from the localizer samples analyses overall shows good spatial correspondence with results from previous meta-analyses and the MMP1 (Glasser et al. 2016), but with some important differences that are worth examining in detail (see Table 3). The FEF ALE peaks from our results are localized much more medially and posteriorly relative to the results reported in Paus (1996), highlighting marked spatial differences with this landmark FEF meta-analysis. In contrast, the IFJ ALE peaks are virtually identical to those reported in the study by Derrfuss et al. (2005; but with slightly less agreement in the right hemisphere), where the authors also employed the ALE technique in one of its earlier implementations. Macro-anatomically, according to the Mindboggle 101 atlas (Klein et al. 2012; Manera et al. 2020), the LH FEF and RH FEF peaks lie within the caudal middle frontal gyrus (in BA 6; see Table 3) and not in the precentral gyrus, as previously assumed based on non-human primate evidence (Bruce et al 1985; Schall et al. 2020, and Tehovnik et al. 2000, for reviews). These results are consistent with the few pieces of evidence available on the delineation of this region based on cytoarchitecture in *post-mortem* studies (Rosano et al. 2003; Schmitt et al. 2005). While the left IFJ ALE peak was found in the precentral gyrus (in BA 6; see Table 3), interestingly the right IFJ ALE peak was instead localized within the pars opercularis (in BA 9). The distinctive architecture of the IFJ remains elusive, but these peaks agree with the general idea that this area is localized in several Brodmann areas (BA6, 8, 9, 44 and 45), and may correspond to a specific cyto- and chemo-architecture found dorsal to BA44 (Amunts and Von Cramon 2006; for a recent fine-grained analysis of its architecture see Ruland et al. 2022).

Table 3 Comparison of the ALE peaks with previous meta-analyses and brain atlases

Cluster	Hemi	ALE peaks						Previous meta-analyses (Talairach space)						Brain atlases		LOEO results
		MNI152 coordinates			Talairach coordinates			Paus (1996)			Derrfuss et al. (2005)			Mindboggle 101	MMP1	
		x	y	z	x	y	z	x	y	z	x	y	z	Label	Label	ALE peak ratio
FEF	L	-28	-6	54	-27.73	-9.61	51.32	-32	-2	46	//	//	//	Caudal Middle Frontal Gyrus	i6-8	26/35
FEF	R	30	-6	50	27.17	-9.86	48.03	31	-2	47	//	//	//	Caudal Middle Frontal Gyrus	6a	23/35
IFJ	L	-42	6	30	-40.87	3.27	30.37	//	//	//	-40	4	30/32	Precentral Gyrus	6r	31/32
IFJ	R	46	12	28	42.43	8.35	29.4	//	//	//	44	10	34	Pars Opercularis	6r	24/32

Finally, in our opinion, the most interesting results of these comparisons were those obtained from the projection of our main FEF and IFJ clusters on the FSaverage surface using the method from Wu et al. (2017) where we could carefully examine their spatial relationship with the MMP1 (Glasser et al. 2016; see Figure 4). The FEF clusters covered almost the entire middle and anterior part of the FEF (as defined by the corresponding MMP1 label) but also large parts of the middle and posterior 6a region. Moreover, the left and right hemisphere ALE peaks were found within area i6-8 and area 6a, anteriorly and dorsally relative to the FEF, respectively. The IFJ clusters instead spanned multiple MMP1 labels, including areas PEF, 6r, IFJp and IFJa. While in the left hemisphere, the majority of the vertices of the cluster were localized in the middle and posterior aspect of the IFJp, in the right hemisphere most of the vertices were localized in the ventral 6r region. Crucially, in both hemispheres, however, the ALE peaks were localized in this region (i.e., 6r), ventrally relative to the IFJp.

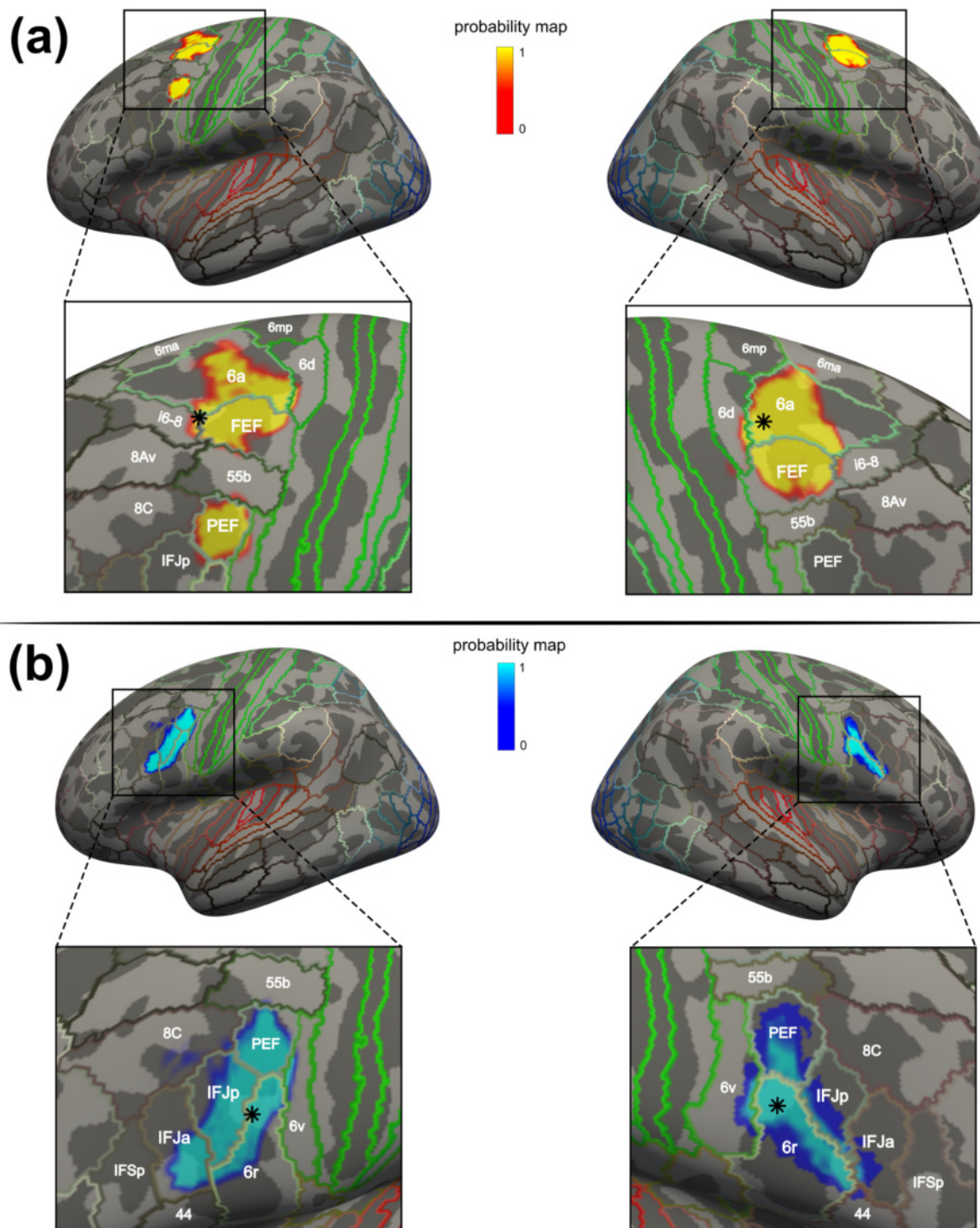


FIGURE 4 Projection on FSaverage of the FEF and IFJ main clusters and comparison with the MMP1 taxonomy. **A** Vertices corresponding to the FEF clusters. Both clusters covered the middle and rostral parts of the FEF label as defined according to the MMP1 atlas, but they also covered large parts of area 6a. In the left hemisphere, vertices were also localized in the iFEF, which matches almost exactly the boundaries of area PEF from the atlas. The LH FEF peak was localized within area i6-8, just anterior to the FEF, and the RH FEF peak was localized within area 6a, dorsal to FEF. Despite this difference, both peaks

were localized near the junction of the sPCS and the SFS, in the anterior bank and the posterior banks of the sPCS, respectively. **B** Vertices corresponding to the IFJ clusters. They showed a similar elongated shape that approximately followed the posterior iPCS and encroached onto the IFS, and they spanned multiple MMP1 areas. Importantly, we found that in both hemispheres the IFJ peaks were localized near the junction of the iPCS and the SFS within area 6r, posteriorly to the IFJp

3.3.5 | Meta-analytic connectivity modeling results

The MACM analysis of the FEF and IFJ revealed a broad set of regions that coactivated with these seeds in the BrainMap database (see Figure 5) encompassing the frontal, parietal and temporal cortices. The LH FEF seed coactivated with other six clusters (see Figure 5, panel A), and the RH FEF coactivated with other eight clusters (Figure 5, panel B). Interestingly, while these FEF coactivations included as expected medial oculomotor regions (the SCEF) and the SPL/IPL, in both analyses we found coactivated clusters in the bilateral ventral PFC, which included parts of the iFEF and the IFJ based on their localization relative to the iPCS and the IFS. The LH IFJ coactivated with a broad set of other nine clusters (Figure 5, panel C), and the RH IFJ coactivated with only five other clusters (Figure 5, panel D). The coactivations of these bilateral seeds spread onto the IFS and ventrally in the insular cortex and claustrum. Again, these coactivations included clusters in the SCEF, the SPL/IPL and the angular gyrus. In contrast to the FEF coactivations, where the bilateral IFJ was always coactivated, we did not find FEF coactivations in the IFJ MACM results, except for the ipsilateral FEF in the LH IFJ MACM analysis. Another crucial difference was that in this analysis, we found a large cluster in the left temporal lobe that included the fusiform gyrus and the inferior occipital cortex. We confirmed these patterns by performing an ALE contrast analysis between the FEF and IFJ MACM results in each hemisphere (see Supplementary Information p. 16). To summarize, while the FEF MACM analysis showed that this region is consistently coactivated with the ventrolateral PFC and regions in the posterior parietal cortex across paradigms, the IFJ had more widespread coactivation patterns (particularly in the LH), being more strongly connected with the rest of the PFC and with the insular cortex and claustrum, and possessing a differential connectivity pattern with regions of the inferior temporal cortex. In contrast, we found differential coactivations of the LH and RH FEF with the ipsilateral precuneus/SPL and lateral intraparietal areas. In addition to revealing the task-based functional connectivity fingerprints of these regions (i.e., the coactivation patterns, as reported above), our functional decoding approach in BrainMap also allowed us to uncover the behavioral domains significantly associated with each of them (Figure 5, right side of each panel; see Supplementary Information p. 16 for a summary of these results).

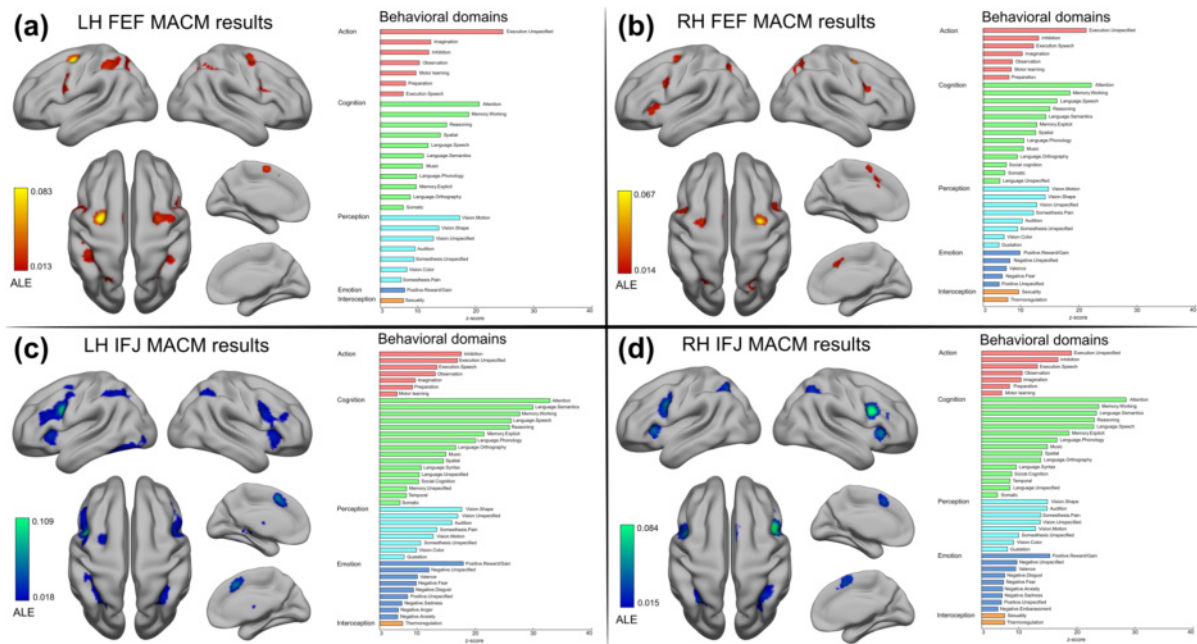


FIGURE 5 Meta-analytic connectivity modeling results. **A** and **B** depict the coactivation profiles of the FEF, and **C** and **D** the coactivation profiles of the IFJ. On the right side of each panel: decoding results of the significant associations with behavioral domains ($p < 0.05$, Bonferroni corrected)

3.4 | DISCUSSION

The PFC is essential to several aspects of flexible goal-driven behavior that are mediated by specialized brain regions (Fuster 2000; Miller and Cohen 2001). The FEF and the IFJ have been previously implicated in covert spatial attention and oculomotor control on the one hand (Corbetta et al. 1998; Vernet et al. 2014), and working memory and cognitive control on the other (Bedini and Baldauf 2021; Brass et al. 2005). Their localization has been traditionally associated with the major sulci of the posterior-lateral PFC, namely the SFS and the sPCS, and the iPCS and the IFS, respectively (Brass et al. 2005; Paus 1996). Due to the large body of empirical work that has accumulated over the past years on these regions (Bedini and Baldauf 2021) and the parallel development of more robust meta-analytic techniques for neuroimaging data (Fox et al. 2014), we felt the need to reassess previous results in light of the current evidence, with a specific focus on overcoming discrepancies in the definition and localization of these regions using fMRI in humans. In particular, in this study, we sought to accurately estimate the precise localization of these regions in standard space by performing a coordinate-based meta-analysis using the ALE technique (Eickhoff et al. 2012). To model the spatial convergence of activations within the FEF, we analyzed data from 35 fMRI studies (35 experiments) that investigated the planning and execution of prosaccades and prosaccades and antisaccades contrasted against a fixation baseline in 449 subjects. To model the spatial convergence within the IFJ, we analyzed data from 30 fMRI studies (32 experiments) that investigated visual attention, working memory, and cognitive control, in 563 subjects. In contrast to previous ALE meta-analyses (Derrfuss et al. 2005; Grosbras et al. 2005; Jamadar et al. 2013) that relied on the false discovery rate, our study

implemented a much more stringent method for multiple comparison correction (i.e., voxel-level FWE). We also included only 3T and 4T fMRI studies to make our inference spatially more reliable. Moreover, testing for significance in each voxel individually enabled us to carry out a fine-grained assessment of activations across experiments. Crucially, we found that by modeling activity across studies (thus partially overcoming inter-individual variability), sulcal landmarks are indeed consistently associated with both regions, as indicated by the location of the ALE peak values (see Figure 1 and Table 3). Our results thus suggest a robust association of structure and function in these higher regions (Frost and Goebel 2012; Miller et al. 2021; Van Essen 2007; Wang et al. 2015), similar to what previous studies have shown in early to mid-level visual regions (Benson et al. 2012; Hinds et al. 2008, 2009). We suggest that this association should be examined by future fMRI studies more systematically at the individual-subject level (Amiez and Petrides 2018; Derrfuss et al. 2009, 2012). Given the limitations of previous meta-analyses (Derrfuss et al. 2005; Grosbras et al. 2005; Jamadar et al. 2013; Paus 1996), we recommend using the coordinates reported in the present study to define FEF and IFJ based on the ALE technique.

The FEF is arguably one of the most important regions of a network involved in the planning and execution of saccadic eye movements and has been extensively studied in primates (Schall and Thompson 1999; Tehovnik et al. 2000). In humans, this network usually comprises a set of regions in the lateral and medial frontal cortex, posterior parietal cortex, and subcortical nuclei (Corbetta et al. 1998; Grosbras et al. 2005), and has been mainly investigated with fMRI over the past 25 years, enabling to characterize their respective functions (McDowell et al. 2008). Following the crucial foundation set by primate neurophysiology (Bruce et al. 1985; Buschman and Miller 2009; Moore and Fallah 2001), the human FEF has often been seen as not only implicated in the production of visually-guided and voluntary saccades and other oculomotor behaviors (Schall 2015), but also covert shifts of spatial attention, spatial working memory, and also more complex executive functions (Corbetta et al. 1998; Fiebelkorn and Kastner 2020; Vernet et al. 2014). Converging lines of research suggest that the FEF works as a spatial priority map (Fiebelkorn and Kastner 2020; Jerde et al. 2012; Sprague and Serences 2013). The localization of the human FEF is however highly debated and affected by strong spatial variability (see Bedini and Baldauf 2021, and Vernet et al. 2014 for a discussion), possibly due to inter-individual differences that are obscured when only reporting group-level results. Previous ALE meta-analyses provided evidence of consistent activations within FEF across PET and fMRI experiments investigating prosaccades and antisaccades (Cieslik et al. 2016; Grosbras et al. 2005; Jamadar et al. 2013). However, given the coarser spatial resolution of PET and low field strength MRI scanners (i.e., 1.5T) and acquisition methods that were included in these previous meta-analyses, these studies were only partially able to accurately infer spatial convergence across experiments, as well as dissociations across paradigms and contrasts. In addition, some of these studies relied on earlier implementations of the ALE technique, which allowed for within-study effects (see Turkeltaub et al. 2012), and critically, more liberal statistical thresholds and multiple comparisons correction solutions (such as false discovery rate, which is no longer recommended, as it is not considered appropriate for spatial inference; Eickhoff et al. 2016). Finally, another aspect that is difficult to evaluate retrospectively was the

reporting of an implementation error in an earlier ALE version (Eickhoff et al. 2017), which affected the meta-analyses previous to that report. In this study, we attempted to overcome some of these limitations by applying a conservative thresholding method and by including higher field fMRI studies (i.e., 3T or 4T) to accurately infer the localization of the human FEF in standard space. Our ALE results, obtained by analyzing prosaccades > fixation, antisaccades > fixation, and prosaccades and antisaccades > fixation contrasts across 35 fMRI experiments (see Table S1), show that the highest spatial convergence based on the ALE value was found within two bilateral clusters in the dorsolateral PFC, localized in the anterior bank of the sPCS, near its junction with the SFS (see Figure 1; Table 2). The comparison with one of the most comprehensive brain parcellations available to date, namely the MMP1 (Glasser et al. 2016), revealed some interesting topographic differences. While many of the projected voxels of our FEF clusters were localized within the middle and anterior part of the MMP1 FEF region, a considerable portion was also spreading dorsally in the middle and posterior 6a region. Furthermore, the ALE peaks were localized within area i6-8 in the left hemisphere, and area 6a in the right hemisphere according to the MMP1. In the left hemisphere, a ventral cluster corresponding to the inferior or lateral FEF (Derrfuss et al. 2012; Kastner et al. 2007; Luna et al. 1998) overlapped almost entirely with the PEF. These results suggest that there may be important differences in the way the FEF is defined across methods. The MMP1 was created by a careful manual delineation combining structural MRI (cortical thickness and myelin ratio), resting-state fMRI connectivity, and retinotopic mapping techniques (Glasser et al. 2016). Additionally, fMRI contrasts from nine tasks were also employed to infer areal boundaries (Barch et al. 2013), which were chosen to optimally balance breadth vs depth and scan time (Elam et al. 2021). Although we regard the MMP1 as a step change in our understanding of brain organization, and in particular of the fine-grained organization and structure of the PFC both in humans and in non-human primates (Donahue et al. 2018), we would like to suggest that more information gathered from task-based fMRI will be needed to better understand the functional subdivision of the plPFC. In particular, following the taxonomy proposed by the MMP1, major efforts should be made to isolate FEF activity from posterior activity in the premotor cortex on the one hand (area 6d), and from a newly discovered language selective region that borders the FEF ventrally on the other, namely area 55b (for a discussion on inter-individual variability in the spatial organization of these regions see Glasser et al. 2016). Ultimately, future developments of a functional localization method will facilitate the convergence of atlas-based and fMRI information to allow the delineation of anatomical clusters of activation within FEF with adequate functional specificity. Our ALE results partly suggest that this is needed as the current gold standard for localizing the FEF may lead to the inclusion of voxels from heterogeneous brain regions as defined according to the MMP1 atlas, possibly also due to the greater inter-subject variability that characterizes the posterior-lateral PFC (Bedini and Baldauf 2021; Glasser et al. 2016).

In this direction, a very compelling set of results were reported by Mackey et al. (2017), who identified two retinotopic maps in the sPCS (sPCS1 and SPC2) and a third one in the iPCS. By examining the correspondences between their results and the MMP1 (see Figure 8 from their study), they found that the sPCS2 corresponded to the FEF, while the sPCS1 corresponded to areas 6a and 6d. Interestingly, they also reported that in all subjects

and both hemispheres, the foveal representation was localized in the fundus of the sPCS, at its intersection with the SFS. This description closely matches the localization of our ALE peaks, which raises the question of whether the fMRI contrasts we included in our meta-analysis could be targeting specific neural populations within the FEF. It is well established that in the macaque, a population of neurons shows increased firing rates when the animal is fixating and is inhibited when executing saccades (hence termed ‘fixation’ neurons; Bruce and Golberg 1985; Hanes et al. 1998; Lowe and Schall 2018). Are these populations of neurons also present in humans, and how are they distributed within the FEF? Are these neurons associated with the significant increase in the BOLD signal when comparing saccades to peripheral positions against a fixation baseline, and what is the role of saccadic amplitude in isolating peaks of activity within the FEF (see Grosbras 2016)? An additional aspect that may be worth investigating is whether the activations found in one or more of these clusters (for example, the iFEF) are dependent on some artifacts present in the experimental design or analysis. In the 35 experiments we analyzed, 10 didn’t record eye movements in the scanner (see Table S1), making it at least likely that some of these clusters were driven by mixed signals and in the worst case, by spurious neural activity that was not related to saccadic behavior. For example, it is well documented that eye blinks can contaminate BOLD signal (Bristow et al. 2005; Hupé et al. 2012), and this fact was invoked to explain discrepancies in the oculomotor organization in primates (Tehovnik et al. 2000) and as a signal driving iFEF responses (Amiez and Petrides 2009; Kato and Miyauchi 2003). In conclusion, we strongly agree with the general caveat that the way the FEF is defined is ultimately constrained by the technique employed (Schall et al. 2020; Vernet et al. 2014), and in particular its spatial resolution. The localization and the extent of the FEF cluster should be inferred based on the convergence of multiple criteria (primarily architectonic, sulcal, functional, connectional, and also comparative). With the present ALE meta-analysis, we aimed at providing updated quantitative evidence on the localization of this region in standard space using standard functional localizers across over 400 subjects. However, additional efforts will be needed to understand the organization of the human eye fields in the PFC and their relationship with sulcal neuroanatomy at the individual-subject level (Amiez et al. 2006; Amiez and Petrides 2018; Frost and Goebel 2012). Careful mapping of the localization of the human FEF is also essential to bridge research in humans and non-human primates and will be crucial for testing hypotheses about homologies in the organization of the prefrontal cortex across species, for example, based on connectivity information (Mars et al. 2021; Neggers et al. 2015; Sallet et al. 2013).

The study of the role of the ventrolateral PFC in various cognitive functions such as non-spatial attention, working memory and cognitive control led to the definition of the IFJ as a separate brain region involved in critical aspects of all these functions (Brass et al. 2005; Derrfuss et al. 2004, 2005). This region seems to be tightly coupled with specific sulcal landmarks across individuals, namely the junction of the iPCS and the IFS (Derrfuss et al. 2009) and belongs to the frontoparietal network (Cole and Schneider 2007; Cole et al. 2013; Yeo et al. 2011). Recent fMRI evidence from a large sample moreover showed that the IFJp is one of the core multiple demand regions of the brain (Assem et al. 2020). In this study, we therefore pooled together results from the various tasks that have been used to localize this

region (see Table S2) ranging from attentional (i.e., RSVP/oddball; Asplund et al. 2010; and endogenous cueing paradigms; Baldauf and Desimone 2014; Zhang et al. 2018), working memory (primarily n-back paradigms; Zanto et al. 2010), and cognitive control paradigms (i.e., task-switching and Stroop tasks; Brass and Von Cramon 2002; Derrfuss et al. 2012). Following a previous meta-analysis (Derrfuss et al. 2005), we reasoned that the spatial convergence across these paradigms (rather than a single task) would allow us to infer the accurate localization of the IFJ in standard space. Consistent with our hypothesis, we found two prominent clusters of activation in the ventral PFC. Based on the respective ALE peak values, the highest convergence was found in the posterior bank of the iPCS, approximately at the height of its ventral junction with the IFS (see Figure 3; Table 2). The comparison of these results with the MMP1 (Glasser et al. 2016) through their projection to the FSaverage surface revealed additional interesting topographic differences. Both IFJ clusters spanned several regions of the MMP1, including areas PEF, 6r, IFJp, and IFJa (Figure 6, panel B), with the majority of the voxels being localized around the borders of IFJp, 6r and the PEF. Moreover, both ALE peaks were localized in area 6r, ventral to the IFJp. These results suggest that the paradigms currently employed to localize the IFJ, and some of those which can be considered promising candidates for this purpose, will also tend to activate voxels from several other brain regions as defined according to this atlas. This problem is further exacerbated by the fact that the IFJp itself and the neighboring regions are also part of the multiple demand system, so many experimental manipulations will tend to coactivate some of them at the same time, thus concealing its boundaries. We examined potential differences in localization between paradigms in a control analysis (see Figure S6 in the Supplementary Information). Taken together, our results showed that oddball/attention paradigms tend to activate voxels that are localized in the posterior aspect of the IFS, whereas both working memory and cognitive control paradigms tend to activate more posterior voxels in the banks of the iPCS. These results seem to suggest that these paradigms consistently recruit different IFJ subregions and additional regions, although their overlap is precisely localized within the IFJ.

An interesting approach that recognizes the integrative nature of the IFJ draws from the combination of different paradigms and uses the conjunction of the respective activations to localize this region, which may overcome some of the previous limitations. Stiers and Goulas (2018) analyzed the voxel responses across three different tasks (Eriksen flanker task, backmatching or n-back task, and a response switching task) to define the prefrontal nodes of the multiple demand system in 12 subjects. A manipulation of task difficulty in each of the previous tasks was used to identify voxels that were modulated by increasing cognitive demands, which were used to define ROIs in each subject in a conjunction analysis across tasks for further analyzing their relative task preference and functional connectivity patterns. Their conjunction analysis revealed local maxima of activity within the IFJ, where voxels with different task preferences exhibited distinct functional connectivity patterns with the rest of the brain (Stiers and Goulas 2018). Based on these results, it may be argued that no single task alone would adequately capture the selectivity patterns of neural populations within the IFJ; rather, manipulations of task difficulty combined with the administration of different tasks could provide an unbiased way of localizing this region in individual participants. The

results of the present study aimed at providing quantitative evidence of the convergence of activations within the IFJ across non-spatial attentional, working memory, and cognitive control tasks across over 500 subjects, which we hope will help guide future research aimed at understanding the relationship between the function and localization of the IFJ, and its relationship with sulcal neuroanatomy at the individual subject level (Derrfuss et al. 2009). Future meta-analyses should better clarify how activations from different tasks that tap cognitive control functions map onto the ventro-lateral PFC and assess whether they may recruit distinct subregions near the IFJ (see for example Kim et al. 2012, and Nee et al. 2013), which was however outside the scope of our present work.

A secondary goal of the present study was to uncover the task-based functional connectivity fingerprint (Passingham et al. 2002) of the FEF and the IFJ in a data-driven fashion. We retrieved in the BrainMap database all the studies that reported activations within a cuboid seed centered around the FEF and IFJ standard coordinates found in our ALE main localizer analyses and we employed the MACM technique (Langner and Camilleri 2021) to uncover their coactivation profiles. Importantly, while previous studies already performed MACM analyses on the FEF (Cieslik et al. 2016) and the IFJ (Muhle-Karbe et al. 2016; Sundermann and Pfeleiderer 2012), our study is to our knowledge the first that used this technique on the results of an ALE analysis specifically aimed at localizing these regions (and not a manual or atlas-based delineation) using a conservative seed extent (6 mm). Our MACM analysis allowed adequately powered inference in each seed region ($n > 17$ experiments; Eickhoff et al. 2016) and revealed broad networks of coactivations that encompassed the frontal, parietal and temporal cortices (see Figure 5). The most remarkable differences between FEF and IFJ coactivation patterns were that on the one hand, the LH and RH FEF coactivated with the bilateral ventrolateral PFC (iFEF and IFJ), whereas only the LH IFJ coactivated with the left FEF in the experiments retrieved. On the other hand, the LH IFJ had stronger and more widespread coactivations in PFC and the insular cortex and was also coactivated with the inferotemporal cortex. These coactivation patterns may be essential for the IFJ to perform its role in feature- and object-based attention tasks (Baldauf and Desimone 2014; Gong and Liu 2020; Meyyappan et al. 2021) and could be in turn supported by its underlying anatomical connectivity patterns (Baldauf and Desimone 2014; Bedini et al. 2021). These results are consistent with the idea of a dorso-ventral segregation of fronto-parietal coactivations forming a spatial/motor and a non-spatial/motor network, and that is in turn associated with the first and third branch of the superior longitudinal fasciculus, respectively (Parlatini et al. 2017). In addition, our functional decoding results suggest that these systematic coactivation patterns allow these regions to support multiple yet specialized roles in flexible goal-driven behavior (Assem et al. 2020; Fiebelkorn and Kastner 2020; Ngo et al. 2019).

3.5 | CONCLUSION

Our study provides the accurate localization of two regions of the posterior lateral PFC, namely the FEF and the IFJ. These regions are tightly linked to sulcal landmarks as measured using fMRI across over 400 hundred subjects, with the FEF being localized at the

junction of the sPCS and the SFS, and the IFJ at the junction of the iPCS and the IFS. Functionally, they appear to be organized according to a dorso-ventral gradient, going from areas responsible for sensorimotor transformations and action execution (FEF, iFEF), to areas that are involved in maintaining and updating behavioral goals according to internal representations (IFJ; Nee et al. 2013; O'Reilly 2010). Taken together, our findings aim at proposing a consensus standard localization of these regions in standard space, and meta-analytic groundwork to investigate the relationship between functional specialization and connectivity in large publicly available neuroimaging datasets (e.g., Markiewicz et al. 2021; Van Essen et al. 2013), as well as to guide future non-invasive brain stimulation studies.

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COMPETING INTERESTS

The authors have no relevant financial or non-financial interests to disclose.

AUTHOR CONTRIBUTIONS

Conceptualization: **MB, DB**; Methodology: **MB, EO, PA, DB**; Software: **MB**; Validation: **MB**; Formal analysis: **MB**; Investigation: **MB**; Resources: **MB, DB**; Data curation: **MB**; Writing - original draft: **MB**; Writing - review and editing: **MB, EO, PA, DB**; Visualization: **MB**; Supervision: **EO, PA, DB**; Project administration: **MB**; Funding acquisition: **MB**.

DATA AVAILABILITY

The FEF and IFJ localizer sample ALE results are available in NeuroVault at: <https://neurovault.org/collections/KLNRWMMU/>.

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3.6 | SUPPLEMENTARY INFORMATION

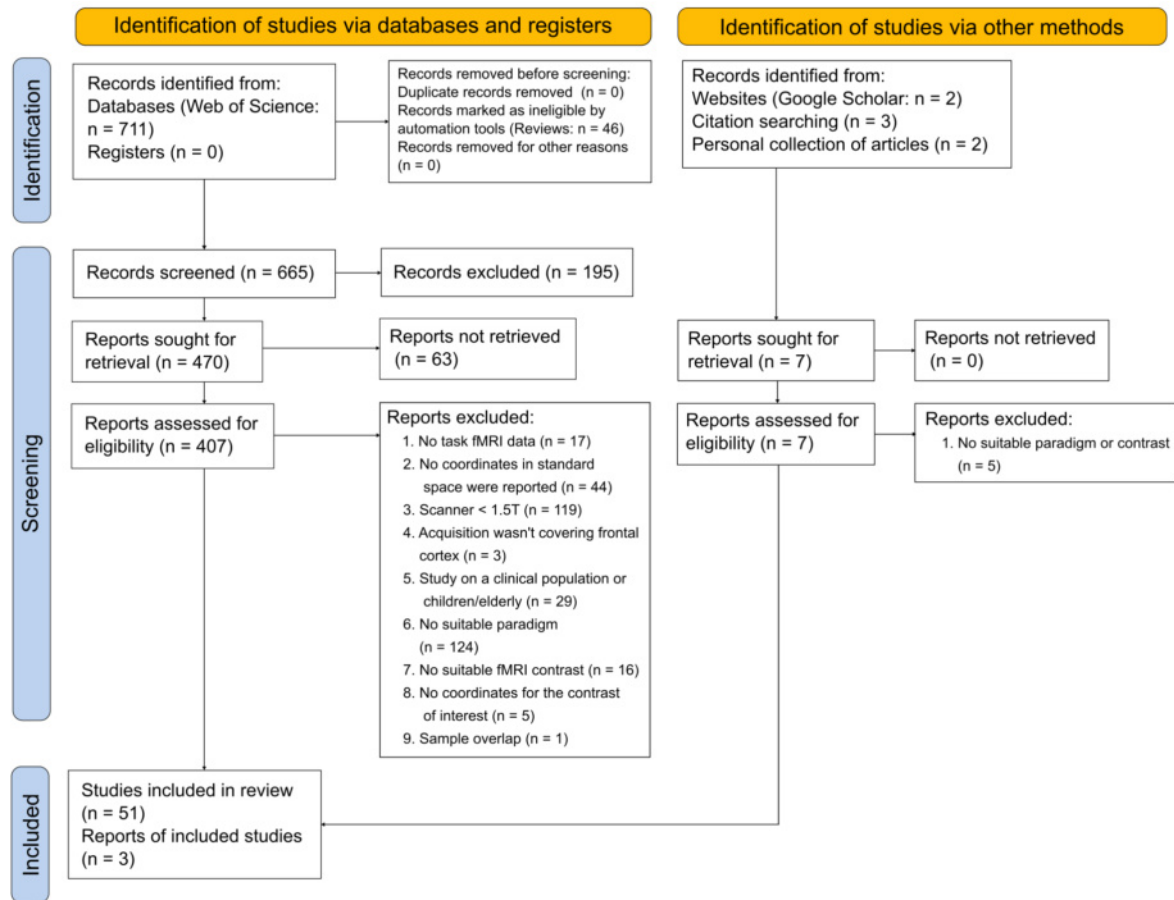


FIGURE S1 PRISMA flow chart FEF sample

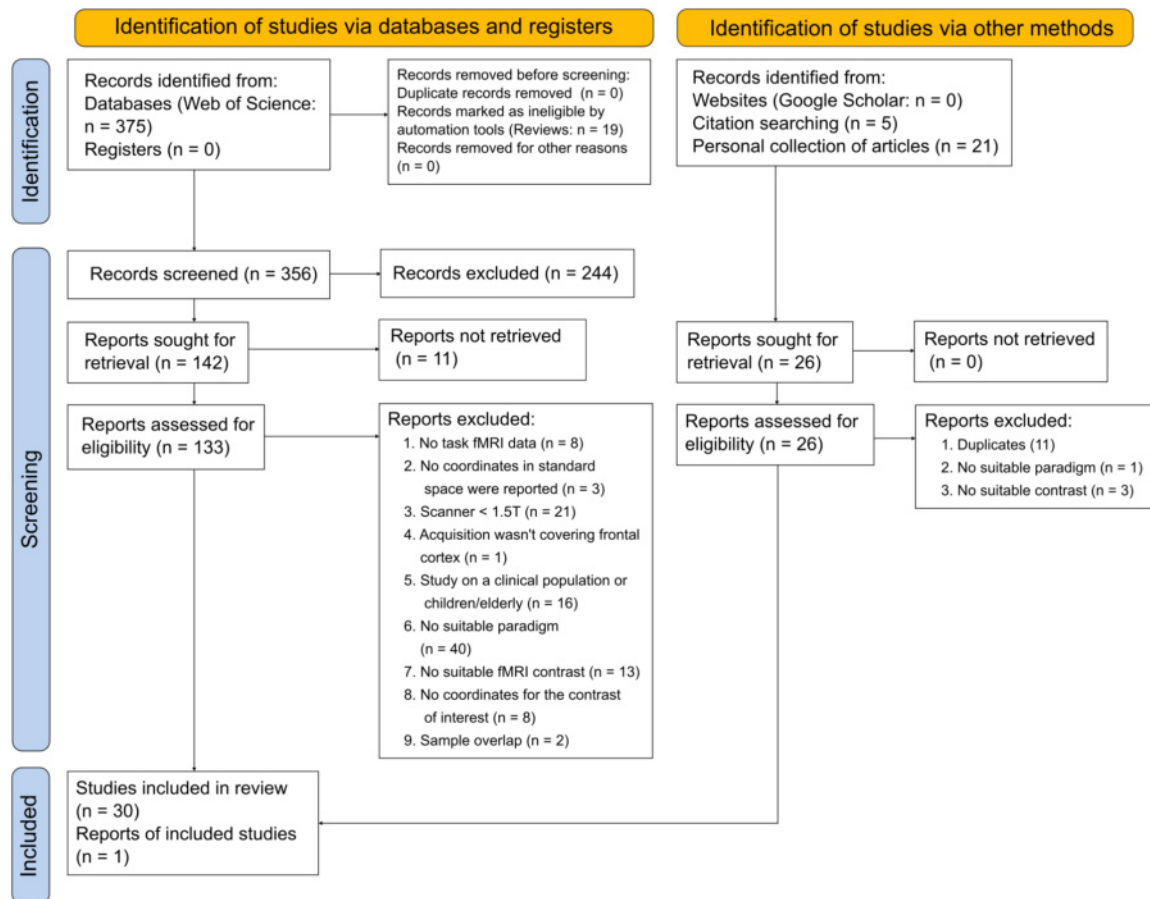


FIGURE S2 PRISMA flow chart IFJ sample

Supplementary Table 1 List of the studies included in the FEF localizer sample

Study	N	Age	Paradigm	Contrast	Scanner	Design	Eye tracker
Alkan et al. (2011)	8	26 ± 4	Oculomotor task	Prosaccades > Fixation	3T	Blocked	Y
Amiez and Petrides (2018)	13	22.6 ± 2.8	Oculomotor task	Prosaccades > Fixation	3T	Blocked	N
Atmaca et al. (2013)	11	26.9; 22-33	Oculomotor task	Prosaccades > Fixation	3T	Blocked	N
Bär et al. (2016)	14	22-56	Oculomotor task	Prosaccades > Fixation	3T	Blocked	N
Bär et al. (2016)	14	22-56	Oculomotor task	Antisaccades > Fixation	3T	Blocked	N
Berman et al. (1999)	11	25.6 ± 7.1; 18-43	Oculomotor task	Prosaccades > Fixation	3T	Blocked	N
Braga et al. (2016)	20	26.2; 21-36	Oculomotor task	Prosaccades > Fixation	3T	Blocked	Y
Brown et al. (2006)	10	26; 22-33	Oculomotor task	Prosaccades > Fixation	4T	<i>Event-related</i>	Y
Brown et al. (2006)	10	26; 22-33	Oculomotor task	Antisaccades > Fixation	4T	<i>Event-related</i>	Y
Connolly et al. (2000)	7	24.8 ± 3.2	Oculomotor task	Prosaccades > Fixation	4T	Blocked	N
Connolly et al. (2000)	7	24.8 ± 3.2	Oculomotor task	Antisaccades > Fixation	4T	Blocked	N
Connolly et al. (2002)	8	NA	Oculomotor task	Prosaccades > Fixation	4T	Blocked	N
Connolly et al. (2005)	5	NA	Oculomotor task	Prosaccades > Fixation	4T	Blocked	Y
Connolly et al. (2007)	8	NA	Oculomotor task	Prosaccades > Fixation	4T	Blocked	N
Christophel et al. (2018)	22	24.4 ± 0.83	Oculomotor task	Prosaccades > Fixation	3T	<i>Event-related</i>	N
Curtis & Connolly (2008)	12	21-35	Oculomotor task	Pro- & Antisaccades > Fixation	3T	<i>Event-related</i>	Y
DeSouza et al. (2003)	10	26.6 ± 1.0	Oculomotor task	Pro- & Antisaccades > Fixation	4T	Blocked	Y
Duecker et al. (2013)	20	19-28	Oculomotor task	Prosaccades > Fixation	3T	Blocked	N
Fernandez-Ruiz et al. (2018)	25	21.7 ± 1.9; 18-25	Oculomotor task	Pro- & Antisaccades > Fixation	3T	<i>Event-related</i>	Y
Fransson et al. (2014)	24	26.7 ± 4.9	Oculomotor task	Prosaccades > Fixation	3T	Blocked	Y
Furlan et al. (2016)	6	NA	Oculomotor task	Pro- & Antisaccades > Fixation	3T	<i>Event-related</i>	Y
Guo et al. (2012)	12	19-31	Oculomotor task	Prosaccades > Fixation	3T	Blocked	Y
Gurel et al. (2018)	16	23.2	Oculomotor task	Prosaccades > Fixation	3T	Blocked	Y
Heinen et al. (2006)	5	20-37	Oculomotor task	Prosaccades > Fixation	3T	Blocked	Y
Hubl et al. (2008)	7	31 ± 9	Oculomotor task	Prosaccades > Fixation	3T	Blocked	N
Jamadar et al. (2015)	23	25.8; 18-43	Oculomotor task	Prosaccades > Fixation	3T	<i>Event-related</i>	Y
Jamadar et al. (2015)	23	25.8; 18-43	Oculomotor task	Antisaccades > Fixation	3T	<i>Event-related</i>	Y
Jarvstad & Gilchrist (2019)	23	NA	Oculomotor task	Prosaccades > Fixation	3T	Blocked	Y
Kastner et al. (2007)	4	20-36	Oculomotor task	Prosaccades > Fixation	3T	Blocked	Y
Kurata et al. (2005)	6	29-38	Oculomotor task	Prosaccades > Fixation	3T	Blocked	N
Levy et al. (2007)	4	24-43	Oculomotor task	Prosaccades > Fixation	3T	Blocked	N
Neggers et al. (2007)	15	NA	Oculomotor task	Pro- & Antisaccades > Fixation	3T	Blocked	N
Pierce et al. (2019)	30	25.7 ± 4.1	Oculomotor task	Prosaccades > Fixation	3T	Blocked	Y
Schon et al. (2008)	17	21.29 ± 3.72	Oculomotor task	Prosaccades > Fixation	3T	Blocked	N
Schwerdtfeger et al. (2013)	14	29.6 ± 9.6	Oculomotor task	Pro- & Antisaccades > Fixation	3T	<i>Event-related</i>	Y
Tamber-Rosenau et al. (2018)	8	28.5 ± 3.3	Oculomotor task	Prosaccades > Fixation	3T	Blocked	Y
Tark & Curtis (2009)	5	22-39	Oculomotor task	Prosaccades > Fixation	3T	Blocked	Y
Tibber et al. (2010)	16	21-40	Oculomotor task	Prosaccades > Fixation	3T	Blocked	Y
Tu et al. (2006)	10	27.9 ± 3.18	Oculomotor task	Antisaccades > Fixation	3T	Blocked	N

Supplementary Table 1 (Continued)

Study	Independent fMRI localizer	Field of View (FOV)	Results reported for	N° of foci	Multiple FEF foci	Software	Space
Alkan et al. (2011)	N	220 mm	Whole-brain	19	N	AFNI	Talairach
Amiez and Petrides (2018)	N	NA	FEF foci	2	N	SPM12b	MNI
Atmaca et al. (2013)	Y	192 mm	Whole-brain	24	Y	SPM8	MNI
Bär et al. (2016)	N	240 mm	Whole-brain	12	N	BrainVoyager QX 1.10	Talairach
Bär et al. (2016)	N	240 mm	Whole-brain	18	Y	BrainVoyager QX 1.10	Talairach
Berman et al. (1999)	N	40 x 20 mm	ROIs	14	Y	AFNI	Talairach
Braga et al. (2016)	Y	220 mm	Whole-brain	7	N	FSL	MNI
Brown et al. (2006)	N	220 mm	Whole-brain	17	N	BrainVoyager 2000	Talairach
Brown et al. (2006)	N	220 mm	Whole-brain	21	N	BrainVoyager 2000	Talairach
Connolly et al. (2000)	N	192 mm	Whole-brain	7	Y	Stimulate	Talairach
Connolly et al. (2000)	N	192 mm	Whole-brain	13	Y	Stimulate	Talairach
Connolly et al. (2002)	Y	192 mm	ROIs	4	N	Stimulate	Talairach
Connolly et al. (2005)	Y	192 mm	ROIs	5	N	Stimulate / BrainVoyager 4.9	Talairach
Connolly et al. (2007)	Y	192 mm	ROIs	2	Y	Stimulate / BrainVoyager 4.9	Talairach
Christophel et al. (2018)	Y	192 mm	FEF foci	2	N	SPM8	MNI
Curtis & Connolly (2008)	N	192 mm	ROIs	32	Y	Caret	MNI
DeSouza et al. (2003)	Y	192 mm	Whole-brain	9	N	BrainVoyager 2000 4.4	Talairach
Duecker et al. (2013)	Y	192 mm	FEF foci	2	N	BrainVoyager QX 2.3	Talairach
Fernandez-Ruiz et al. (2018)	N	211 mm	Whole-brain	18	N	BrainVoyager QX 2.8.4	Talairach
Fransson et al. (2014)	N	288 mm	Whole-brain	8	N	SPM8	MNI
Furlan et al. (2016)	N	192 mm	ROIs	6	N	BrainVoyager QX 2.3	Talairach
Guo et al. (2012)	Y	192 mm	ROIs	6	N	SPM8	Talairach
Gurel et al. (2018)	Y	192 mm	FEF foci	2	N	BrainVoyager QX	Talairach
Heinen et al. (2006)	Y	NA	ROIs	4	N	VISTASOFT	Talairach
Hubl et al. (2008)	Y	192 mm	Whole-brain	9	N	BrainVoyager QX	Talairach
Jamadar et al. (2015)	Y	192 mm	Whole-brain	47	N	SPM8	MNI
Jamadar et al. (2015)	Y	192 mm	Whole-brain	47	N	SPM8	MNI
Jarvstad & Gilchrist (2019)	N	192 mm	Whole-brain	4	N	FSL v.5.06-1	MNI
Kastner et al. (2007)	Y	256 mm	ROIs	5	N	AFNI	Talairach
Kurata et al. (2005)	N	220 mm	Whole-brain	14	N	Advanced Visual Systems & AFNI	Talairach
Levy et al. (2007)	Y	192 mm	ROIs	5	N	BrainVoyager QX	Talairach
Neggens et al. (2007)	Y	224 x 256 x 128 mm	ROIs	4	Y	SPM2	MNI
Pierce et al. (2019)	Y	NA	Whole-brain	9	Y	SPM12	MNI
Schon et al. (2008)	Y	200 mm	Whole-brain	19	N	SPM2	MNI
Schwerdtfeger et al. (2013)	N	211 x 211 mm	ROIs	10	Y	BrainVoyager QX 1.9	Talairach
Tamber-Rosenau et al. (2018)	Y	240 x 240 mm	ROIs	6	N	BrainVoyager QX v.1.10.2–2.8	Talairach
Tark & Curtis (2009)	Y	192 mm	FEF foci	2	N	Caret	MNI
Tibber et al. (2010)	Y	192 mm	ROIs	9	N	SPM5	Talairach
Tu et al. (2006)	Y	250 x 250 mm	Whole-brain	21	N	SPM2	MNI

Supplementary Table 2 List of the studies included in the IFJ localizer sample

Study	N	Age	Paradigm	Contrast	Scanner	Design	Eye tracker
Armbruster et al. (2012)	20	23.5; 20–32	Task-switching paradigm	Task switch > Distractor trials	3T	<i>Event-related</i>	N
Armbruster et al. (2012)	20	23.5; 20–32	Task-switching paradigm	Distractor inhibition > Baseline	3T	<i>Event-related</i>	N
Armbruster et al. (2012)	20	23.5; 20–32	Task-switching paradigm	Task switch > Repetition trials	3T	<i>Event-related</i>	N
Asplund et al. (2010)	30	NA	RSVP / Oddball paradigm	Surprise > Search trials	3T	<i>Event-related</i>	N
Asplund et al. (2010)	30	NA	RSVP / Oddball paradigm	Search trials > Baseline	3T	<i>Event-related</i>	N
Asplund et al. (2010)	6	NA	RSVP / Oddball paradigm	Search trials > Baseline	3T	<i>Event-related</i>	N
Asplund et al. (2010)	6	NA	RSVP / Oddball paradigm	Surprise > Search trials	3T	<i>Event-related</i>	N
Baldauf and Desimone (2014)	12	23-37	Object-based attention paradigm	Attend face/house blocks > Difficulty-matched rare target detection	3T	Blocked	N
Bode and Haynes (2009)	12	26.4; 24-30	Task-switching paradigm	Cue presentation > Baseline	3T	<i>Event-related</i>	N
Bode and Haynes (2009)	12	26.4; 24-30	Task-switching paradigm	Target presentation > Baseline	3T	<i>Event-related</i>	N
Bode and Haynes (2009)	12	26.4; 24-30	Task-switching paradigm	Response > Baseline	3T	<i>Event-related</i>	N
Bollinger et al. (2010)	18	23.4 ± 3.06; 18-28	Working memory paradigm	FC with FFA: Stimulus known > Stimulus unknown	3T	<i>Event-related</i>	N
Bollinger et al. (2010)	18	23.4 ± 3.06; 18-28	Working memory paradigm	FC with FFA: Stimulus known > Passive view + stimulus unknown	3T	<i>Event-related</i>	N
Brass and Von Cramon (2002)	11	26.2 ± 3.06	Task-switching paradigm	Cue-only trials > Null events	3T	<i>Event-related</i>	N
Brass and Von Cramon (2002)	11	26.2 ± 3.06	Task-switching paradigm	Cue-target > Cue-only trials	3T	<i>Event-related</i>	N
Brass and Von Cramon (2002)	11	26.2 ± 3.06	Task-switching paradigm	Cue-target trials > Null events	3T	<i>Event-related</i>	N
Brass and Von Cramon (2002)	11	26.2 ± 3.06	Task-switching paradigm	Cue-target trials > No-cue-target trials	3T	<i>Event-related</i>	N
Brass and Von Cramon (2004)	14	24.4 ± 1.9	Task-switching paradigm	Meaning switch > Cue switch trials	3T	<i>Event-related</i>	N
Brass and Von Cramon (2004)	14	24.2 ± 1.9	Task-switching paradigm	Cue switch > Cue repetition trials	3T	<i>Event-related</i>	N
Brass and Von Cramon (2004)	14	24.4 ± 1.9	Task-switching paradigm	Switch > Repetition trials (single cue)	3T	<i>Event-related</i>	N
Chen et al. (2013)	23	21 ± 1.67	Stroop paradigm	Stimulus incongruent > Congruent trials (early stage)	3T	<i>Event-related</i>	N
Chen et al. (2013)	23	21 ± 1.67	Stroop paradigm	Response incongruent > Stimulus incongruent (early stage)	3T	<i>Event-related</i>	N
Chen et al. (2013)	23	21 ± 1.67	Stroop paradigm	Response incongruent > Stimulus incongruent (late stage)	3T	<i>Event-related</i>	N
Cole and Schneider (2007)	9	19-42	Working memory paradigm	Target switching > Non-switching trials (target non-occluded)	3T	Mixed blocked/event-related	N
Cole and Schneider (2007)	9	19-42	Working memory paradigm	Target switching > Non-switching trials (target occluded)	3T	Mixed blocked/event-related	N
Corradi-Dell'Acqua et al. (2015)	18	28; 18-52	Object-based attention paradigm	High saliency unattended > attended stimuli	3T	<i>Event-related</i>	N
Derrfuss and Von Cramon (2004)	19	20-36	Task-switching paradigm	Switch > Null event trials	3T	<i>Event-related</i>	N
Derrfuss and Von Cramon (2004)	19	20-36	Stroop paradigm	Incongruent > Neutral trials	3T	<i>Event-related</i>	N
Derrfuss and Von Cramon (2004)	19	20-36	Working memory paradigm	2-back > 0-back blocks	3T	Blocked	N
Derrfuss et al. (2012)	12	25.3 ± 2.4; 22-31	Stroop paradigm	Incongruent > Congruent trials	3T	<i>Event-related</i>	N
Han and Marois (2013)	14	20-32	RSVP paradigm	Discontinuous > Continuous & continuous-hard conditions	3T	<i>Event-related</i>	N
Han and Marois (2014)	14	20-32	RSVP / Oddball paradigm	Single-short oddball trials > Search no-target trials	3T	<i>Event-related</i>	N
Han and Marois (2014)	14	20-32	RSVP / Oddball paradigm	Target > Distractor trials	3T	<i>Event-related</i>	N
Han and Marois (2014)	6	19-35	RSVP / Oddball paradigm	Target > Distractor trials	3T	<i>Event-related</i>	N
Han et al. (2018)	20	22-33	RSVP / Oddball paradigm	Oddball > Search trials	3T	<i>Event-related</i>	N
Harding et al. (2016)	25	25.5 ± 4.4	Working memory paradigm	2-back > 0-back trials (main effect)	3T	<i>Event-related</i>	N
Henseler et al. (2011)	27	24.56 ± 2.53	Working memory paradigm	External attending to targets > Baseline	3T	Blocked	N
Henseler et al. (2011)	27	24.56 ± 2.53	Working memory paradigm	Internal orienting > Baseline	3T	Blocked	N
Henseler et al. (2011)	27	24.56 ± 2.53	Working memory paradigm	Internal > External attending (position task)	3T	Blocked	N
Kim et al. (2012)	16	23.6 ± 2.9; 18-35	Task-switching paradigm	Task switch > Non-switch trials (main effect)	3T	<i>Event-related</i>	N
Kim et al. (2012)	16	23.6 ± 2.9; 18-35	Stroop paradigm	Incongruent > Congruent trials (main effect)	3T	<i>Event-related</i>	N
Lin et al. (2019)	18	27.4 ± 6.6	Working memory paradigm	FC face cue and target > FC scene cue and target	3T	<i>Event-related</i>	Y
Melcher and Gruber (2006)	12	25.67 ± 1.88	Stroop paradigm	Incongruent > Congruent trials	3T	<i>Event-related</i>	N
Melcher and Gruber (2006)	12	25.67 ± 1.88	Oddball paradigm	Word-oddball vs. Oddball control	3T	<i>Event-related</i>	N
Melcher and Gruber (2006)	12	25.67 ± 1.88	Oddball paradigm	Color-oddball vs. Oddball control	3T	<i>Event-related</i>	N
Roth et al. (2006)	12	23; 19-34	Working memory paradigm	Sustained working memory > Sustained feature detection	3T	Blocked	N
Roth et al. (2006)	12	23; 19-34	Working memory paradigm	Update > Cued maintenance	3T	<i>Event-related</i>	N
Sreenivasan et al. (2014)	16	22; 18-32	Working memory paradigm	Memory > Rotation discrimination trials	3T	Blocked	N
Stelzel et al. (2011)	48	F: 22 ± 1.99; M: 22.6 ± 1.99	Task-switching paradigm	Task switch > Repetition trials	3T	<i>Event-related</i>	N
Todd et al. (2011)	18	18-31	Working memory paradigm	Encoding period > Baseline	3T	<i>Event-related</i>	N
Wills et al. (2017)	22	18-30	Contingent capture paradigm	Salient target > Baseline	3T	<i>Event-related</i>	N
Yin et al. (2017)	26	21.3; 21-25	Task-switching paradigm	Task switch > Repetition trials	3T	<i>Event-related</i>	N
Zanto et al. (2010)	13	25; 20-31	Working memory paradigm	FC with V4: Attend > Ignore color	3T	<i>Event-related</i>	N
Zanto et al. (2010)	13	25; 20-31	Working memory paradigm	FC with V5: Attend > Ignore motion	3T	<i>Event-related</i>	N
Zanto et al. (2011)	20	24.25; 18-31	Working memory paradigm	FC with V4: Attend > Ignore color	3T	<i>Event-related</i>	N
Zanto et al. (2011)	20	24.25; 18-31	Working memory paradigm	FC with V5: Attend > Ignore motion	3T	<i>Event-related</i>	N
Zhang et al. (2018)	19	19-26	Feature-based attention paradigm	Stimulus block > Baseline	3T	Blocked	Y
Zhao et al. (2020)	13	21.54 ± 1.99	Working memory paradigm	High working memory load > Low working memory load	3T	<i>Event-related</i>	N

Supplementary Table 2 (Continued)

Study	Independent fMRI localizer	Field of View (FOV)	Results reported for	N° of foci	IFJ's activity lateralization	Software	Space
Armbruster et al. (2012)	N	192 mm	Whole-brain	15	Bilateral	SPM8	MNI
Armbruster et al. (2012)	N	192 mm	Whole-brain	9	Bilateral	SPM8	MNI
Armbruster et al. (2012)	N	192 mm	Whole-brain	13	Left	SPM8	MNI
Asplund et al. (2010)	N	240 mm	Whole-brain	17	Bilateral	BrainVoyager 4.9.1, QX 1.7.9	Talairach
Asplund et al. (2010)	N	240 mm	Whole-brain	8	Bilateral	BrainVoyager 4.9.1, QX 1.7.9	Talairach
Asplund et al. (2010)	N	240 mm	ROIs	8	Bilateral	BrainVoyager QX 1.11.4	Talairach
Asplund et al. (2010)	N	240 mm	ROIs	8	Bilateral	BrainVoyager QX 1.11.4	Talairach
Baldauf and Desimone (2014)	Y	N/A	IFJ only	2	Bilateral	SPM8	MNI
Bode and Haynes (2009)	N	N/A	Whole-brain	7	NA	SPM2	MNI
Bode and Haynes (2009)	N	N/A	Whole-brain	12	NA	SPM2	MNI
Bode and Haynes (2009)	N	N/A	Whole-brain	9	NA	SPM2	MNI
Bollinger et al. (2010)	N	230 mm	Whole-brain	17	Right	SPM5	MNI
Bollinger et al. (2010)	N	230 mm	Whole-brain	17	Right	SPM5	MNI
Brass and Von Cramon (2002)	N	192 mm	Whole-brain	22	Bilateral	LIPSIA	Talairach
Brass and Von Cramon (2002)	N	192 mm	Whole-brain	21	Left	LIPSIA	Talairach
Brass and Von Cramon (2002)	N	192 mm	Whole-brain	10	Bilateral	LIPSIA	Talairach
Brass and Von Cramon (2002)	N	192 mm	Whole-brain	9	Bilateral	LIPSIA	Talairach
Brass and Von Cramon (2004)	N	192 mm	ROIs	3	Left	LIPSIA	Talairach
Brass and Von Cramon (2004)	N	192 mm	ROIs	4	NA	LIPSIA	Talairach
Brass and Von Cramon (2004)	N	192 mm	ROIs	3	Left	LIPSIA	Talairach
Chen et al. (2013)	N	250 x 250 mm	Whole-brain	10	NA	SPM8	Talairach
Chen et al. (2013)	N	250 x 250 mm	Whole-brain	5	NA	SPM8	Talairach
Chen et al. (2013)	N	250 x 250 mm	Whole-brain	9	NA	SPM8	Talairach
Cole and Schneider (2007)	N	210 mm	Whole-brain	12	Bilateral	BrainVoyager QX	Talairach
Cole and Schneider (2007)	N	210 mm	Whole-brain	5	NA	BrainVoyager QX	Talairach
Corradi-Dell'Acqua et al. (2015)	N	N/A	Whole-brain	5	Bilateral	SPM8	MNI
Derrfuss and Von Cramon (2004)	N	192 mm	IFJ only	2	Bilateral	LIPSIA	Talairach
Derrfuss and Von Cramon (2004)	N	192 mm	IFJ only	2	Bilateral	LIPSIA	Talairach
Derrfuss and Von Cramon (2004)	N	192 mm	IFJ only	2	Bilateral	LIPSIA	Talairach
Derrfuss et al. (2012)	N	220 x 220 mm	IFJ only	1	Left	FSL	MNI
Han and Marois (2013)	Y	240 mm	Whole-brain	14	Bilateral	BrainVoyager QX 1.10	Talairach
Han and Marois (2014)	N	240 mm	Whole-brain	7	Bilateral	BrainVoyager QX 2.3	Talairach
Han and Marois (2014)	N	240 mm	Whole-brain	11	Bilateral	BrainVoyager QX 2.3	Talairach
Han and Marois (2014)	N	240 mm	Whole-brain	11	Bilateral	BrainVoyager QX 2.3	Talairach
Han et al. (2018)	N	240 mm	Whole-brain	6	Bilateral	FSL	MNI
Harding et al. (2016)	N	210 x 210 mm	Whole-brain	21	Bilateral	SPM8	MNI
Henseler et al. (2011)	N	192 mm	Whole-brain	7	NA	SPM2	MNI
Henseler et al. (2011)	N	192 mm	Whole-brain	8	NA	SPM2	MNI
Henseler et al. (2011)	N	192 mm	Whole-brain	15	Bilateral	SPM2	MNI
Kim et al. (2012)	N	224 mm	Whole-brain	20	Left	SPM5	MNI
Kim et al. (2012)	N	224 mm	Whole-brain	22	Bilateral	SPM5	MNI
Lin et al. (2019)	N	220 mm	Whole-brain	9	Right	FSL	MNI
Melcher and Gruber (2006)	N	192 mm	Whole-brain	13	NA	SPM2	MNI
Melcher and Gruber (2006)	N	192 mm	Whole-brain	19	Bilateral	SPM2	MNI
Melcher and Gruber (2006)	N	192 mm	Whole-brain	29	Bilateral	SPM2	MNI
Roth et al. (2006)	N	N/A	Whole-brain	15	Left	AFNI	Talairach
Roth et al. (2006)	N	N/A	Whole-brain	11	Left	AFNI	Talairach
Sreenivasan et al. (2014)	N	N/A	ROIs	13	Right	AFNI	Talairach
Stelzel et al. (2011)	N	240 mm	Whole-brain	5	Left	SPM5	MNI
Todd et al. (2011)	N	240 mm	Whole-brain	27	Bilateral	BrainVoyager QX v.1.09	Talairach
Wills et al. (2017)	N	220 mm	ROIs	13	Bilateral	AFNI	Talairach
Yin et al. (2017)	N	192 mm	Whole-brain	15	Left	SPM8	MNI
Zanto et al. (2010)	Y	230 mm	Whole-brain	5	Right	SPM5	MNI
Zanto et al. (2010)	Y	230 mm	Whole-brain	8	Bilateral	SPM5	MNI
Zanto et al. (2011)	Y	230 mm	Whole-brain	18	Right	SPM5	MNI
Zanto et al. (2011)	Y	230 mm	Whole-brain	16	Bilateral	SPM5	MNI
Zhang et al. (2018)	N	192 mm	ROIs	8	Bilateral	BrainVoyager QX	Talairach
Zhao et al. (2020)	N	210 mm	Whole-brain	7	Bilateral	SPM8	MNI

3.6.1 | ALE control and contrast analyses method

We carried out two control analyses in the FEF and IFJ localizer samples to rule out potential biases in our main results. As we were mainly interested in inferring the localization of the FEF and IFJ, we decided to include studies with partial brain coverage. We motivated this choice by accepting the tradeoff between having access to a larger sample of experiments for these regions, as opposed to having less sensitivity in detecting other regions that are consistently active during the tasks included (which however are not the main focus of the present study), but not reported simply due to the lack of whole-brain brain coverage. The inclusion of studies with partial brain coverage is however generally not recommended in ALE analyses (Müller et al. 2018). In our first set of control analyses, we have therefore excluded those studies based on the FOV parameters reported in the study (see Tables S1 and S2) or the author's description of the fMRI data acquisition. This led to the exclusion of two experiments from the FEF sample (namely Amiez and Petrides 2018, and Berman et al. 1999), and one study in the IFJ sample (Sreenivasan et al. 2014). For this control analysis, the ALE parameters were set to 5000 threshold permutations and a voxel-level FWE of 0.01 with a minimum cluster size of 50mm³ (corresponding to 6 voxels). The second set of control analyses was carried out to rule out another potential source of biases, that is, ROI analyses (Müller et al. 2018). These analyses imply restricting the assessment of statistical significance by some form of spatial masking. In this case, we excluded all the studies that either carried out ROI analyses or that only reported their results for specific ROIs (or even only FEF and IFJ foci; see Tables S1 and S2, column "Results reported for"). This led to an important decrease in both the FEF and IFJ localizer sample sizes (to 16 and 22 eligible experiments, respectively). Again, the ALE parameters were set to 5000 threshold permutations and a voxel-level FWE of 0.01 with a minimum cluster size of 50mm³ (corresponding to 6 voxels), as in our main localizer analyses.

As we were also interested in exploring potential dissociations in the prefrontal cortex, we carried out several ALE contrast analyses. For all these contrast analyses, we first computed separate ALE results for each function or contrast of interest by setting the ALE parameters to 10000 threshold permutations and a cluster-level FWE of 0.01 with $p < 0.001$. The experiments included in either analysis were randomly split into two groups of equal size to run a third pooled ALE analysis using the same parameters. The ALE scores of these two groups were then subtracted voxel-wise from each other 10000 times to create a null distribution of the difference between them. We used a threshold of $p < 0.01$ to infer significant differences between the two groups with a minimum cluster size of 25 mm³ (as in Cieslik et al. 2016). The voxel-wise minimum of the ALE scores between the samples was used to create the conjunction image that indicates the similarity between the two groups of experiments.

3.6.2 | ALE control and contrast analyses - FEF sample

1. **Cluster-level FWE control analysis.** In our main FEF localizer analysis, we applied voxel-level FWE correction, as this method allowed us a fine-grained assessment of

the significant activations near the FEF. However, in the case of regions that are under-reported in the literature (i.e., the iFEF; Derrfuss et al. 2012), the use of a voxel-level FWE correction method may impose a too-conservative threshold that would prevent us from detecting clusters of activity that are also consistently activated in the FEF localizer sample. For instance, this could be due to the fact that most studies where an FEF functional localizer was employed tend to report only a pair of bilateral foci, leaving out other regions potentially active in the task (see Table S1 for the studies that have only reported part of their results), thus biasing the results in favor of the main activation cluster. In this first control analysis, we applied a less stringent multiple comparison correction method in order to reveal other consistently active peaks in neighboring frontal sites, namely cluster-level FWE. This correction method offers an optimal balance between sensitivity and specificity in ALE analyses to detect regions that may be under-reported (Eickhoff et al. 2016). As we introduced above, since the iFEF is under-reported in the fMRI literature, we hypothesized that this control analysis could be helpful in uncovering these activations. We therefore repeated the same ALE procedure on the FEF localizer sample setting the ALE parameters to a p-value of 0.001, with 10000 threshold permutations and applying a cluster-level FWE of 0.01.

2. **ALE contrast analysis - antisaccades vs prosaccades.** The second control analysis was intended as a replication of the ALE meta-analysis by Cieslik et al. (2016), who performed an ALE contrast analysis between experiments investigating prosaccades > fixation vs antisaccades > prosaccades in two equal samples of 12 experiments (see also Jamadar et al. 2013, for previous results). We note that, unlike Cieslik et al. (2016), we did not include PET studies, and also 1.5T fMRI studies to increase the spatial accuracy of our analysis (see the Supplementary Table 4 below for the details of the experiments included).
3. **ALE contrast analysis - prosaccades vs covert spatial attention.** In our main localizer analysis, we did not include covert spatial attention tasks as these aren't considered the gold standard to localize the FEF. However, covert spatial attention paradigms are often employed to localize all the main nodes of the dorsal attention network, including the FEF (Corbetta and Shulman 2002). Therefore, studies using adaptations of the spatial cueing paradigm (Posner et al. 1980) were included in this analysis (see Supplementary Table 5). Running a contrast analysis between prosaccades and covert spatial attention paradigm allowed us to compare the topography and the sources of overt and covert attention near the putative FEF. For this analysis, we used prosaccades > fixation vs valid > neutral/invalid trials contrasts.

3.6.3 | ALE contrast analyses - IFJ sample

Given the heterogeneity of the experiments included in the IFJ localizer sample, we carried out exploratory ALE contrast analyses by splitting up the IFJ sample according to the function investigated by each paradigm (i.e., oddball/attention vs working memory vs

task-switching and Stroop paradigms; see Table S2) to see whether these paradigms elicited activity in distinct regions near the putative IFJ and to assess potential lateralization patterns. Task-switching and Stroop paradigms were grouped based on the results from Derrfuss et al. (2005), and we refer to this group of experiments as targeting cognitive control. In the first group of experiments (oddball/attention), most of the oddball experiments contrasted oddball > target trials and target trials > baseline (see for example Asplund et al. 2010), thus tapping on both stimulus-driven and goal-driven attentional mechanisms. There were also some examples of blocked design cueing paradigms contrasting target vs fixation blocks (Baldauf and Desimone 2014; Zhang et al. 2018). In the working memory group, the majority of experiments contrasted the functional connectivity between perceptual seed regions (V4, V5, FFA) in the attended vs ignored conditions (see for example Bollinger et al. 2010; Lin et al. 2019; Zanto et al. 2010, 2011). We note that even though these studies were based on a second-level contrasts analysis, and thus involve some form of masking (i.e., the restriction to a specific brain region for the assessment of the significance level, hence spatial bias), the significant correlations with each seed were assessed over the whole-brain, making the localization of the IFJ with this method likely only slightly affected by this issue, if at all. Indeed, as previously suggested in Nee et al. (2013), their results match well those from traditional univariate analyses. The cognitive control group was mostly composed of experiments contrasting switch > repeat trials and incongruent > congruent contrasts in Stroop paradigms.

We therefore ran three separate ALE contrast analyses:

1. **Oddball/attention vs working memory** (11 vs 12 experiments):
2. **Working memory vs cognitive control** (12 vs 11 experiments), and;
3. **Oddball/attention vs cognitive control** (11 vs 11 experiments).

Supplementary Table 3 List of the experiments included in the prosaccade > fixation analysis

Study	N	Age	Paradigm	Contrast	Scanner	Design
Alkan et al. (2011)	8	26 ± 4	Functional localizer	Prosaccades > Fixation	3T	Blocked
Amiez and Petrides (2018)	13	22.6 ± 2.8	Functional localizer	Prosaccades > Fixation	3T	Blocked
Atmaca et al. (2013)	11	26.9; 22-33	Functional localizer	Prosaccades > Fixation	3T	Blocked
Bär et al. (2016)	14	22-56	Functional localizer	Prosaccades > Fixation	3T	Blocked
Berman et al. (1999)	11	25.6 ± 7.1; 18-43	Functional localizer	Prosaccades > Fixation	3T	Blocked
Braga et al. (2016)	20	26.2; 21-36	Functional localizer	Prosaccades > Fixation	3T	Blocked
Brown et al. (2006)	10	26; 22-33	Functional localizer	Prosaccades > Fixation	4T	<i>Event-related</i>
Connolly et al. (2000)	7	24.8 ± 3.2	Functional localizer	Prosaccades > Fixation	4T	Blocked
Connolly et al. (2002)	8	NA	Functional localizer	Prosaccades > Fixation	4T	Blocked
Connolly et al. (2005)	5	NA	Functional localizer	Prosaccades > Fixation	4T	Blocked
Connolly et al. (2007)	8	NA	Functional localizer	Prosaccades > Fixation	4T	Blocked
Christophel et al. (2018)	22	24.4 ± 0.83	Functional localizer	Prosaccades > Fixation	3T	<i>Event-related</i>
Duecker et al. (2013)	20	19-28	Functional localizer	Prosaccades > Fixation	3T	Blocked
Fransson et al. (2014)	24	26.7 ± 4.9	Functional localizer	Prosaccades > Fixation	3T	Blocked
Guo et al. (2012)	12	19-31	Functional localizer	Prosaccades > Fixation	3T	Blocked
Gurel et al. (2018)	16	23.2	Functional localizer	Prosaccades > Fixation	3T	Blocked
Heinen et al. (2006)	5	20-37	Functional localizer	Prosaccades > Fixation	3T	Blocked
Hubl et al. (2008)	7	31 ± 9	Functional localizer	Prosaccades > Fixation	3T	Blocked
Jamadar et al. (2015)	23	25.8; 18-43	Functional localizer	Prosaccades > Fixation	3T	<i>Event-related</i>
Jarvstad & Gilchrist (2019)	23	NA	Functional localizer	Prosaccades > Fixation	3T	Blocked
Kastner et al. (2007)	4	20-36	Functional localizer	Prosaccades > Fixation	3T	Blocked
Kurata et al. (2005)	6	29-38	Functional localizer	Prosaccades > Fixation	3T	Blocked
Levy et al. (2007)	4	24-43	Functional localizer	Prosaccades > Fixation	3T	Blocked
Matsuo et al. (2003)	12	20-42	Functional localizer	Prosaccades > Fixation	3T	Blocked
Pierce et al. (2019)	30	25.7 ± 4.1	Functional localizer	Prosaccades > Fixation	3T	Blocked
Schon et al. (2008)	17	21.29 ± 3.72	Functional localizer	Prosaccades > Fixation	3T	Blocked
Tamber-Rosenau et al. (2018)	8	28.5 ± 3.3	Functional localizer	Prosaccades > Fixation	3T	Blocked
Tark & Curtis (2009)	5	22-39	Functional localizer	Prosaccades > Fixation	3T	Blocked
Tibber et al. (2010)	16	21-40	Functional localizer	Prosaccades > Fixation	3T	Blocked

Supplementary Table 3 (Continued)

Study	Eye tracker	Results reported for	N° of foci	Multiple FEF foci	Software	Space
Alkan et al. (2011)	Y	Whole-brain	19	N	AFNI	Talairach
Amiez and Petrides (2018)	N	FEF foci	2	N	SPM12b	MNI
Atmaca et al. (2013)	N	Whole-brain	24	Y	SPM8	MNI
Bär et al. (2016)	N	Whole-brain	12	N	BrainVoyager QX 1.10	Talairach
Berman et al. (1999)	N	ROIs	14	Y	AFNI	Talairach
Braga et al. (2016)	Y	Whole-brain	7	N	FSL	MNI
Brown et al. (2006)	Y	Whole-brain	17	N	BrainVoyager 2000	Talairach
Connolly et al. (2000)	N	Whole-brain	7	Y	Stimulate	Talairach
Connolly et al. (2002)	N	ROIs	4	N	Stimulate	Talairach
Connolly et al. (2005)	Y	ROIs	5	N	Stimulate / Brain Voyager 4.9	Talairach
Connolly et al. (2007)	N	ROIs	2	Y	Stimulate / BrainVoyager 4.9 / QX	Talairach
Christophel et al. (2018)	N	FEF foci	2	N	SPM8	MNI
Duecker et al. (2013)	N	FEF foci	2	N	BrainVoyager QX 2.3	Talairach
Fransson et al. (2014)	Y	Whole-brain	8	N	SPM8	MNI
Guo et al. (2012)	Y	ROIs	6	N	SPM8	Talairach
Gurel et al. (2018)	Y	FEF foci	2	N	BrainVoyager QX	Talairach
Heinen et al. (2006)	Y	ROIs	4	N	VISTASOFT	Talairach
Hubl et al. (2008)	N	Whole-brain	9	N	BrainVoyager QX	Talairach
Jamadar et al. (2015)	Y	Whole-brain	47	N	SPM8	MNI
Jarvstad & Gilchrist (2019)	Y	Whole-brain	4	N	FSL v.5.06-1	MNI
Kastner et al. (2007)	Y	ROIs	5	N	AFNI	Talairach
Kurata et al. (2005)	N	Whole-brain	14	N	Advanced Visual Systems & AFNI	Talairach
Levy et al. (2007)	N	ROIs	5	N	BrainVoyager QX	Talairach
Matsuo et al. (2003)	N	FEF foci	1	N	SPM99	MNI
Pierce et al. (2019)	Y	Whole-brain	9	Y	SPM12	MNI
Schon et al. (2008)	N	Whole-brain	19	N	SPM2	MNI
Tamber-Rosenau et al. (2018)	Y	ROIs	6	N	BrainVoyager QX v.1.10.2–2.8	Talairach
Tark & Curtis (2009)	Y	FEF foci	2	N	Caret	MNI
Tibber et al. (2010)	Y	ROIs	9	N	SPM5	Talairach

Supplementary Table 4 List of the experiments included in the antisaccades > prosaccade analysis

Study	N	Age	Paradigm	Contrast	Scanner	Design
Brown et al. (2006)	10	26; 22-33	Antisaccade paradigm	Antisaccades > Prosaccades trials	4T	<i>Event-related</i>
Brown et al. (2007)	11	25; 20-28	Antisaccade paradigm	Antisaccades > Prosaccades trials	4T	<i>Event-related</i>
Brown et al. (2007)	11	25; 20-28	Antisaccade paradigm	Antisaccades > Prosaccades trials	4T	<i>Event-related</i>
Cameron et al. (2009)	11	22-30	Antisaccade paradigm	Antisaccades > Prosaccades trials	3T	<i>Event-related</i>
Ford et al. (2005)	10	28	Antisaccade paradigm	Antisaccades > Prosaccades trials	4T	<i>Event-related</i>
Manoach et al. (2007)	21	34.2 ± 12.6	Antisaccade paradigm	Antisaccades > Prosaccades trials	3T	<i>Event-related</i>
Neggers et al. (2012)	13	20-35	Antisaccade paradigm	Antisaccades > Prosaccades trials	3T	<i>Event-related</i>
Peirce & McDowell (2016)	35	19 ± 3.5	Antisaccade paradigm	Antisaccades > Prosaccades trials	3T	<i>Event-related</i>
Peirce & McDowell (2017)	35	19 ± 3.5	Antisaccade paradigm	Antisaccades > Prosaccades blocks	3T	Blocked
Salvia et al. (2020)	14	27.1 ± 2.7	Antisaccade paradigm	Antisaccades > Prosaccades trials	3T	<i>Event-related</i>

Supplementary Table 4 (Continued)

Study	Eye tracker	Results reported for	N° of foci	Software	Space
Brown et al. (2006)	Y	Whole-brain	15	BrainVoyager 2000	Talairach
Brown et al. (2007)	Y	Whole-brain	14	BrainVoyager 2000	Talairach
Brown et al. (2007)	Y	Whole-brain	11	BrainVoyager 2000	Talairach
Cameron et al. (2009)	Y	FEF foci	2	BrainVoyager 1.9	Talairach
Ford et al. (2005)	Y	Whole-brain	8	BrainVoyager 2000 v. 4.8	Talairach
Manoach et al. (2007)	Y	Whole-brain	7	FreeSurfer	Talairach
Neggers et al. (2012)	N	ROIs	13	SPM5	MNI
Peirce & McDowell (2016)	Y	Whole-brain	5	AFNI	Talairach
Peirce & McDowell (2017)	Y	Whole-brain	2	AFNI	Talairach
Salvia et al. (2020)	Y	Whole-brain	12	SPM12	MNI

Supplementary Table 5 List of the experiments included in the endogenous covert spatial attention analysis

Study	N	Age	Paradigm	Contrast	Scanner	Design
Chica et al. (2013)	18	25 ± 4	Spatial cueing	Cue > Jitter Fixation	3T	<i>Event-related</i>
Fan et al. (2005)	16	27.2 ± 5.7	Attentional network test	Spatial > Center cue	3T	<i>Event-related</i>
Ikkai & Curtis (2008)	14	21-35	Attentional cueing	Covert shift > Baseline	3T	<i>Event-related</i>
Mao et al. (2007)	12	24.3; 21-27	Spatial cueing	Attention to peripheral locations > Fixation	3T	Blocked
Mohanty et al. (2009)	13	27 ± 3.8	Spatial cueing / Visual search	Valid > Neutral trials	3T	<i>Event-related</i>
Vossel et al. (2012)	24	26.83; 20-37	Spatial cueing	Valid trials > Baseline	3T	<i>Event-related</i>
Wen et al. (2012)	12	20-28	Spatial cueing	Attend > Passive viewing blocks	3T	Blocked
Xuan et al. (2016)	24	26.3; 18-49	Attentional network test	Valid > Invalid trials	3T	<i>Event-related</i>

Supplementary Table 5 (Continued)

Study	Eye tracker	Results reported for	N° of foci	Multiple FEF foci	Software	Space
Chica et al. (2013)	N	Whole-brain	22	Y	SPM5	MNI
Fan et al. (2005)	N	Whole-brain	8	N	SPM99	MNI
Ikkai & Curtis (2008)	Y	ROIs	11	Y	Caret	MNI
Mao et al. (2007)	N	Whole-brain	6	N	SPM99	Talairach
Mohanty et al. (2009)	Y	Whole-brain	10	N	SPM5	MNI
Vossel et al. (2012)	Y	Whole-brain	6	N	SPM8	MNI
Wen et al. (2012)	N	ROIs	7	N	SPM2	MNI
Xuan et al. (2016)	N	Whole-brain	20	N	SPM8	MNI

3.6. | ALE control analyses results

The results of the first control analysis, in which we excluded studies with partial brain coverage, replicated our main localizer results both in terms of the inferred ALE peaks and the number and anatomical localization of the significant clusters. In the FEF sample, the ALE peaks coincided with the main analysis, and the only difference that emerged was a minor shift of the left iFEF peak (from MNI152: -48, -2, 40 to -46, -2, 38). In the IFJ sample, the ALE peaks again coincided with the results of our main analysis.

The results of the second control analysis where we excluded all ROI analyses again matched well with our main results in terms of the inferred ALE peaks but had important differences regarding the number and anatomical localization of the significant clusters. The results of this control analysis are reported in Table S6 and Table S7 for the FEF and IFJ samples, respectively.

In the FEF sample, the cluster with the highest ALE value was now localized primarily in the left medial frontal gyrus, including the SCEF. The second and third clusters larger clusters were however again localized in the left and right FEF respectively and were approximately of the same size. In terms of the inferred FEF ALE peaks, these were almost identical to our main results (LH main: -28, -6, 54 vs no ROI control: -28, -6, 56; and RH main: 30, -6, 50 vs no ROI control: 28, -6, 50; all the coordinates are in MNI152 space). However, in contrast to our main analysis results, the left FEF cluster did not spread onto the iPCS and there wasn't any peak corresponding to the iFEF. Interestingly, we also found a second peak in the right FEF cluster, which was lateral relative to the first, although still localized within the sPCS (MNI152: 40, -4, 50). Similar to the main results, there were other two clusters localized in the left and right precuneus and SPL, but we didn't find evidence of a cluster in the right IPL, possibly due to the lower sample size (35 vs 16 experiments).

In the IFJ sample, the larger clusters were localized in the left and right IFJ, replicating our main analysis results. Their ALE peak exactly matched those from our main results in the left hemisphere (-42, 6, 30) but had some slight differences in the right hemispheres, where we found two peaks with similar ALE values (main: 46, 12, 28 vs no ROI control: 46, 10, 26, and 42, 8, 30; all the coordinates are in MNI152 space). This indicates some residual variability in the localization of the right IFJ, which wasn't detectable in our main analysis results. The remaining clusters were similar to the main analysis results, with the exception that the cluster in the left SPL/IPL was now disjointed into two smaller clusters.

Supplementary Table 6 FEF sample no ROI control analysis ALE results

Cluster	Macroanatomical location	Hemi	MNI152 coordinates			ALE value	Volume (mm ³)	BA
			x	y	z			
1	Medial Frontal Gyrus	L/R	-2	0	58	0.0386	1360	6
2	Precentral Gyrus	L	-28	-6	56	0.0341	992	6
3	Middle Frontal Gyrus	R	28	-6	50	0.0308	960	6
	Precentral Gyrus	R	40	-4	50	0.0275		6
4	Precuneus	L	-22	-58	56	0.0306	488	7
5	Precuneus	R	26	-60	56	0.0223	112	7

Supplementary Table 7 IFJ sample no ROI control analysis ALE results

Cluster	Macroanatomical location	Hemi	MNI152 coordinates			ALE value	Volume (mm ³)	BA
			x	y	z			
1	Precentral Gyrus	L	-42	6	30	0.0532	2632	6
2	Inferior Frontal Gyrus	R	46	10	26	0.0402	1672	9
	Precentral Gyrus	R	42	8	30	0.0389		6
3	Medial Frontal Gyrus	L	-2	18	46	0.0462	1656	6
4	Precentral Gyrus	L	-28	-4	54	0.0474	816	6
5	Clastrum	R	32	22	-4	0.0348	456	*
6	Precuneus	L	-26	-66	44	0.0302	456	7
7	Inferior Parietal Lobule	L	-32	-54	48	0.0348	384	7
8	Superior Parietal Lobule	R	34	-54	46	0.0323	312	7
9	Clastrum	L	-30	18	2	0.0317	264	*

3.6.5 | ALE control and contrast analyses - FEF sample results

By repeating the ALE analysis using cluster-level FWE instead of voxel-level FWE, we were able to uncover bilateral activations ventral to the main FEF ALE peaks. These activations were extending from the sPCS to the posterior bank of the iPCS and were primarily localized in the iPCS (see Figure S3), corresponding to the iFEF (Kastner et al. 2007). This highlights the fact that, although these clusters may be under-reported in the literature (Derrfuss et al. 2012), they were nevertheless consistently activated in our sample of experiments.

Our two ALE contrast analyses show evidence of important spatial segregation and overlap within FEF for antisaccades, prosaccades and covert spatial attention contrasts (see Figures S4 and S5). Starting with the first contrast analysis, we would like to comment separately on the ALE results for antisaccades > prosaccades and the ‘pure’ prosaccade > fixation results, as these give important clues on how to interpret the ALE peaks from our main analysis results (where we also included ‘mixed’ antisaccades & prosaccades > fixation and antisaccades > fixation contrasts to increase our sample size). In the prosaccades >

fixation ALE results the FEF peaks were localized in: LH 1st ALE peak (-28, -6, 54); LH 2nd ALE peak (-52, 0, 40); RH 1st ALE peak (36, -4, 52); RH 2nd ALE peak (30, -4, 50); RH 3rd ALE peak (34, -2, 50). While the left hemisphere peaks match the main analysis results, in the right hemisphere the strongest convergence is now found more lateral compared to the main result ALE peak (30, -6, 50) suggesting a higher variability along this axis (see Figure S4, Panel A). In the antisaccades > prosaccades ALE results there were only two peaks localized within FEF, specifically in LH (-26, -2, 56), and RH (-28, -2, 54). These peaks were localized more anteriorly and medially compared to our main results (Figure S4, Panel B). This already suggests that there may be important dissociations between the activations derived from these contrasts. Indeed, when we directly contrasted these two samples, we found that the antisaccades > prosaccades and prosaccades > fixation experiments consistently activated segregated prefrontal clusters, as previously reported by other studies (Cieslik et al. 2016; Jamadar et al. 2013). While in the right hemisphere, the antisaccade cluster was medial relative to the prosaccade cluster, and largely overlapping at the junction of the sPCS with the SFS, this organization was less evident in the left hemisphere, where the two clusters overlapped near the same anatomical location, but with a segregated cluster for antisaccades localized in its anterior-medial part (see Figure S4, Panel C). Overall, these results suggest that the additional processes required for the antisaccade task (Munoz and Everling 2004), namely response inhibition and the execution of a saccade towards the opposite location relative to the target, consistently recruit the medial part of the FEF (McDowell et al. 2008). These processes may be mediated by distinct neural populations within the FEF (see Lowe and Schall 2018, for a classification in the macaque). We also found two bilateral segregated clusters in the medial prefrontal cortex for prosaccades localized in the posterior SCEF. The antisaccades clusters were instead localized in the right anterior SCEF. We did not find clusters in the posterior parietal cortex as in Cieslik et al. (2016), with the exception of a cluster in the left precuneus/SPL, possibly due to the fact that our antisaccade sample was lower compared to that study (8 vs 12 experiments), and the influence of studies only reporting ROI analyses.

Our second ALE contrast analysis, namely between prosaccades and covert spatial attention activations (Figure S5, Panel C) reveals a clear pattern of overlap near the junction of the sPCS and SFS. These results are consistent with the hypothesis that covert and overt attention have a spatially common source within the FEF (Astafiev et al. 2003; Corbetta et al. 1998; de Haan et al. 2008). We also found evidence of segregated clusters, with covert attention clusters being mostly localized in the posterior bank of the sPCS in the right and to a smaller extent in the left hemispheres (not visible in Figure S5). These results strongly suggest that covert spatial attention paradigms may be equally adept as FEF functional localizers compared to the current prosaccade gold standard, although more trials may be needed to reliably elicit activations in all subjects due to the weaker nature of the signal measured (Beauchamp et al. 2001; De Haan et al. 2008).

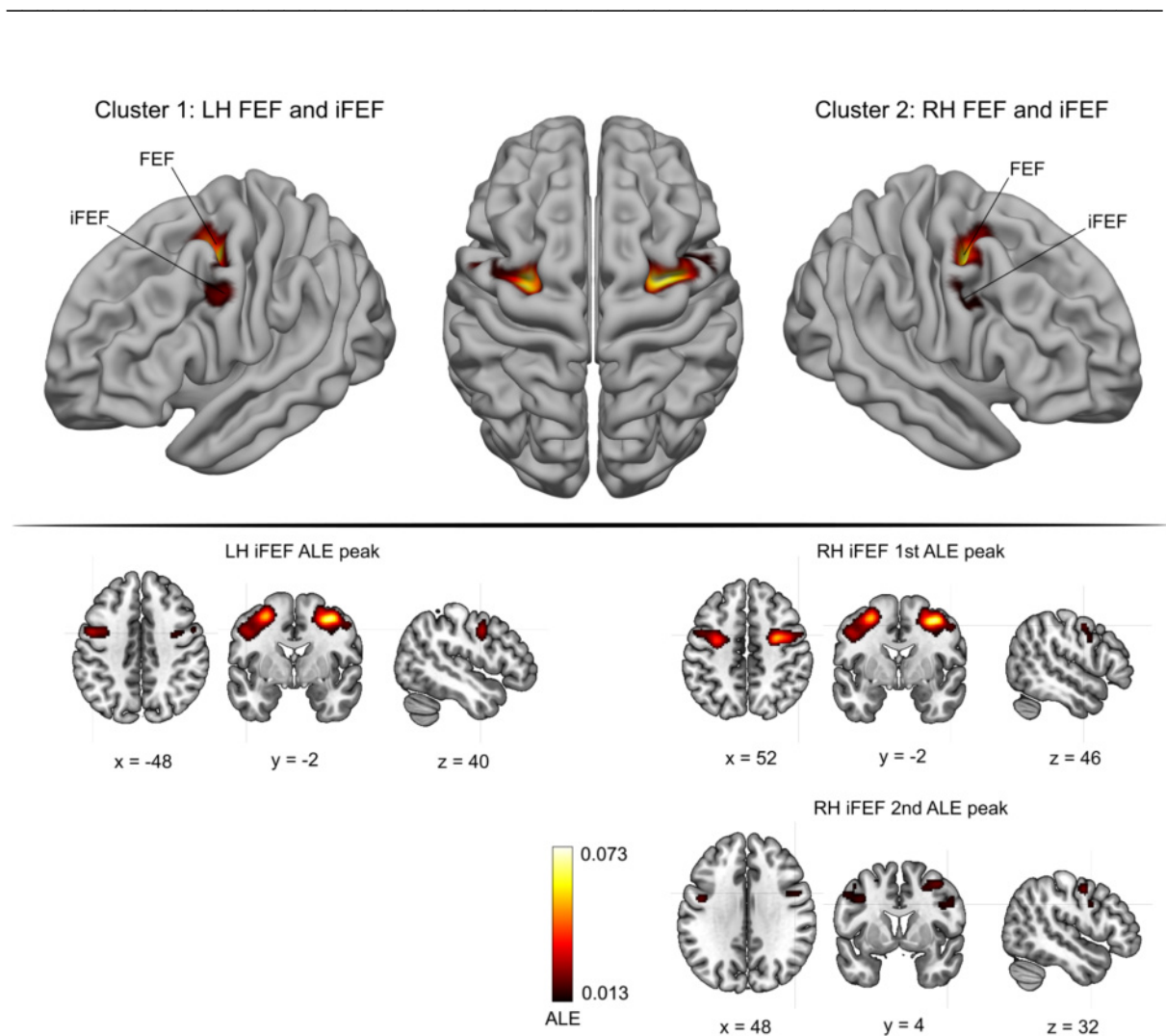


FIGURE S3 Results of the first FEF sample control analysis - main clusters of activation. Applying cluster-level FWE in the ALE analysis allowed us to uncover bilateral activations ventral to the main FEF peaks. These activations were extending from the sPCS to the posterior bank of the iPCS, and were primarily localized in the precentral gyrus. These results reveal the presence of consistent iFEF activations in the FEF localizer sample and three iFEF peaks (shown in the volumetric views of the figure)

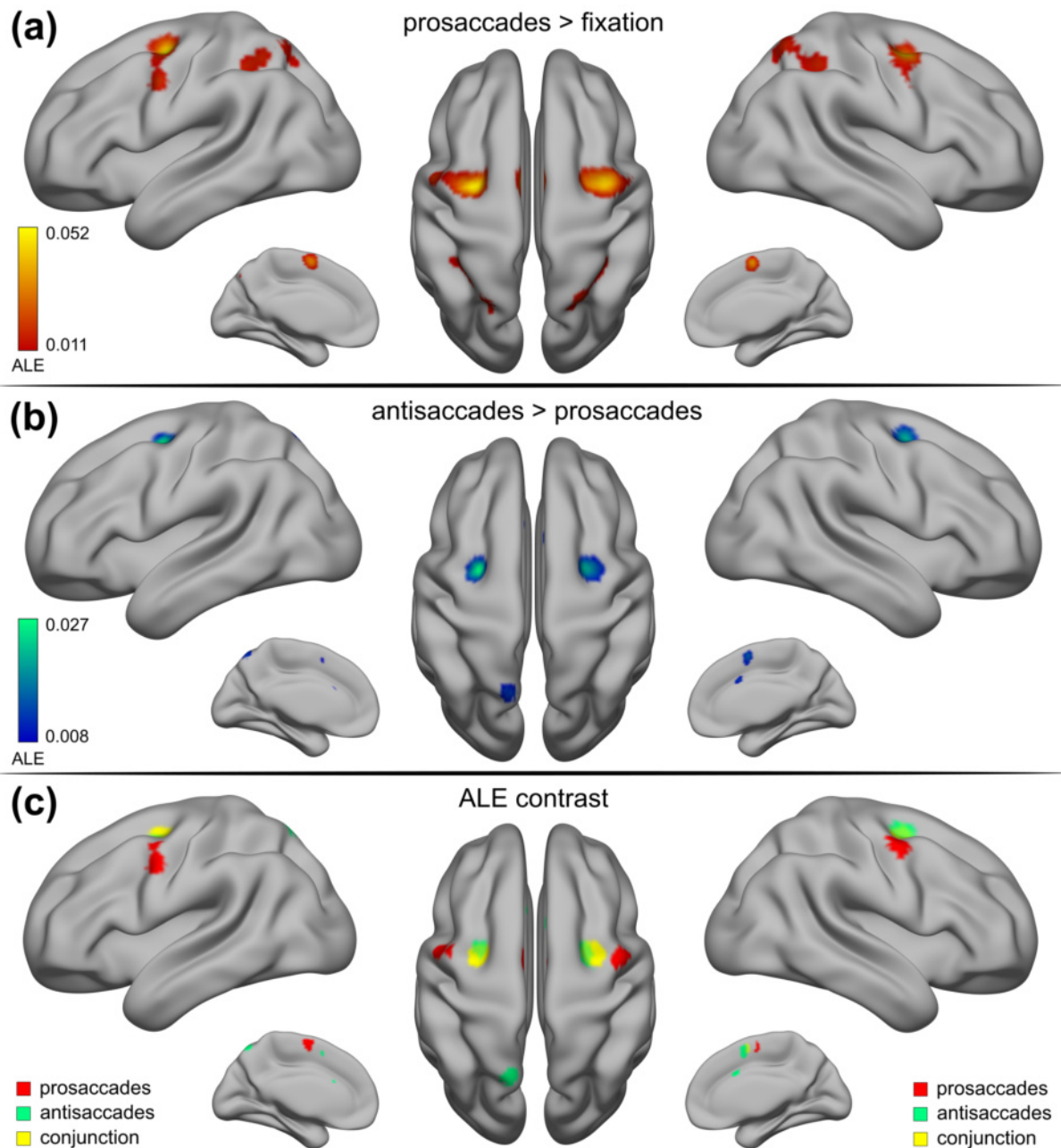


FIGURE S4 FEF sample contrast analysis between antisaccades > prosaccades vs prosaccades > fixation contrasts. **C** The clusters overlap in the bilateral posterior aspect of the SFS and sPCS. The contrast of these clusters showed that the antisaccades-related clusters were generally more medial and localized anterior to the prosaccades-related clusters. These results are consistent with those reported by Cieslik et al. (2016) and suggest that the additional mechanisms required for the antisaccade task are mediated by separate neural populations within the medial aspect of the FEF

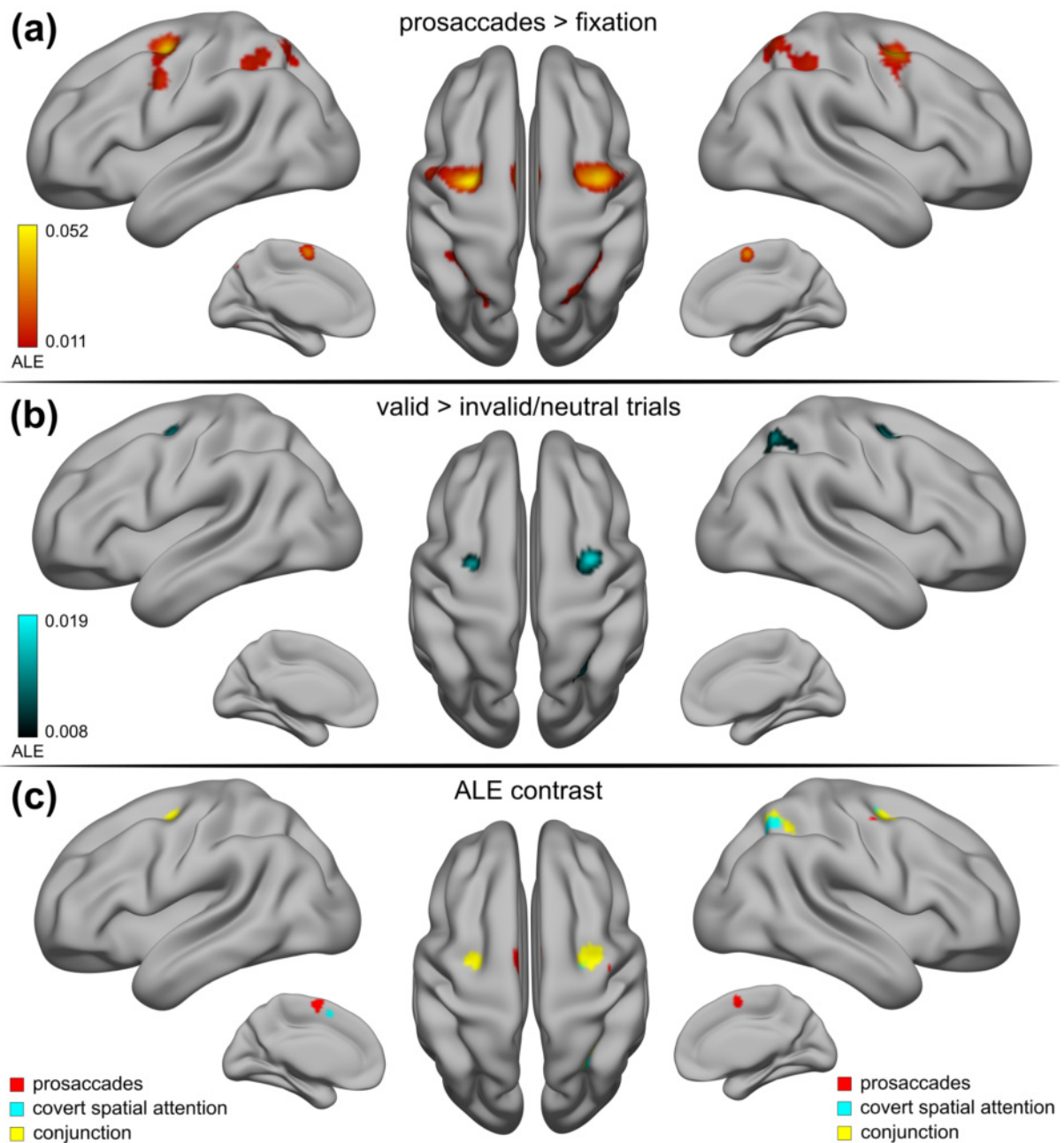


FIGURE S5 FEF sample contrast analysis between prosaccades > fixation vs valid > neutral/invalid trials in covert spatial attention task. **C** The clear overlap we found at the junction of the SFS and sPCS supports the hypothesis that covert and overt attention have a spatially common source within the FEF (Astafiev et al. 2003; Corbetta et al. 1998; de Haan et al. 2008)

3.6.6 | ALE contrast analyses - IFJ sample results

By splitting up our IFJ localizer sample based on the paradigm employed (i.e., oddball/attention vs working memory vs cognitive control), we found some dissociations within the putative IFJ, as well as interesting lateralization patterns (see Figure S6). While oddball/attention paradigms gave rise to bilateral activations near the putative IFJ, working memory paradigms consistently activated only a right hemisphere cluster, whereas in contrast cognitive control paradigms were only consistently activating on a cluster in the left hemisphere. Remarkably, each of these clusters had a quite distinct spatial topography. In the left hemisphere, the cluster related to cognitive control (task-switching and Stroop paradigms) extended from the posterior bank of the superior iPCS to the junction of the iPCS with the IFS, where it overlapped with the oddball/attention cluster (see Figure S6, Panel A). This cluster further extended anteriorly and ventrally. The same arrangement was approximately found in the right hemisphere, in which a posterior-dorsal working memory limited cluster overlapped with the oddball/attention cluster just above the junction of the iPCS with the IFS (see Figure S6, Panel B). The oddball/attention cluster again extended anteriorly and ventrally. Finally, the contrast between working memory and cognitive control only revealed overlap in the left paracentral and midcingulate cortex, as the other clusters were localized within the right and left hemispheres, respectively (see Figure S6, Panel C).

Based on the results from these ALE contrast analyses and their comparisons with our main results, we would like to offer some suggestions on how to effectively localize the IFJ and segregate it from adjacent brain regions. First of all, at the general level, contrasts involving two demanding experimental conditions (e.g., task switch > repeat trials) may be more appropriate to measure activity within the IFJ compared to experimental trials vs passive fixation conditions. Secondly, an even more stringent way to isolate this region would be to compare experimental conditions that are matched in difficulty, thus avoiding contamination from non-specific cognitive load effects (as in Baldauf and Desimone 2014). Oddball/attention paradigms seemed to tap on the same IFJ cluster as found in our main localizer (see Figure S6, Panel A). However, in the experiments we analyzed, these tasks usually contrast activity between oddball and target trials, leading to a low number of trials that are used as functional localizers within each run as a result (Han and Marois 2014). An additional problem may be caused by spatial smoothing, which would lead to merging activity with the IFG, a node classically viewed as belonging to the ventral attention network (Corbetta and Shulman 2002), which is also significantly activated in these paradigms (Levy and Wagner 2011). Therefore, a more straightforward way to isolate the IFJ from the IFG may be achieved by administering top-down feature- and object-based attention tasks (Baldauf and Desimone 2014; Liu et al. 2011; Liu 2016; Zhang et al. 2018) and contrasting valid > invalid trials collapsed across the stimuli features/dimensions (e.g., similarly to the approach reported in Zanto et al. 2010). Posteriorly, another important issue is how to segregate IFJ activity from the iFEF (or the PEF in the MMP1 taxonomy). Derrfuss et al. (2012) reported that by employing a Stroop paradigm and contrasting incongruent > congruent trials, they were able to isolate activity from the adjacent iFEF (which was activated by the execution of voluntary saccades in darkness) in the native space in all the

subjects they analyzed. These results show a promising way to infer the posterior IFJ functional border. As suggested previously however in the case of the FEF results, the presence of significant voxels within the iFEF is particularly difficult to interpret given that, in the IFJ localizer sample, only two out of 32 experiments (see Table S2) employed strict monitoring of eye movements in the scanner. The possibility that the convergence in iFEF in this sample may be due to this confound cannot be therefore completely ruled out (Amiez and Petrides 2009; Kato and Miyauchi 2003). Therefore we suggest that future localization approaches aimed at separating IFJ and iFEF activations must ensure a robust way to prevent data contamination from oculomotor artifacts. Finally, as suggested in our Discussion, the combination of different tasks and the manipulation of task difficulty seems a promising approach to delineate the IFJ based on a conjunction analysis (as in Stiers and Goulas 2018).

3.7.7 | MACM contrast analysis results

To quantitatively examine the dissociations in the MACM patterns of FEF and IFJ for each hemisphere, we also ran an ALE contrast analysis between the LH FEF vs LH IFJ, and RH FEF vs RH IFJ coactivation patterns. Our results generally confirm what can be seen in Figure 5. The LH IFJ coactivated with the RH IFJ and the LH FEF, whereas the LH FEF coactivated with the RH FEF, and LH and RH IFJ. The LH IFJ had also additional coactivations with the insular cortex. Medially, there was a posterior cluster in the SCEF differentially coactivated with the LH FEF, and two clusters in the anterior and mid cingulate cortex coactivated with the LH IFJ. Posteriorly, we found common activations in the IPL, but crucially, dissociations in the precuneus/SPL (for LH FEF) and the fusiform face complex, areas TE2p and V8, and the parahippocampal areas (for the LH IFJ). We found similar results in the right hemisphere. The RH FEF coactivated with the LH FEF, and the LH and RH IFJ. The RH IFJ only coactivated with the LH IFJ and had additional coactivations with the insular cortex. There were differential coactivations of the RH FEF with the precuneus/SPL and the lateral intraparietal area and common coactivations in the left SPL.

3.6.8 | MACM decoding results

Performing a reverse inference on the coactivation patterns of the LH FEF showed that the prevalent association was in the ‘action’ behavioral domain (see Figure 5, right side of panel A), namely *execution.unspecified*. In the ‘cognition’ domain, there were four prominent associations with attention, working memory, reasoning and spatial cognition. Finally, in the ‘perception’ domain, the two highest associations were with *vision.motion* and *vision.shape*. The behavioral domain associations with the coactivation patterns of the RH FEF (see Figure 5, right side of panel B) were very similar to the LH FEF. Again, the primary association in the ‘action’ domain was with *execution.unspecified*. The prevalent association was however in the ‘cognition’ domain with attention, followed by working memory, *language.speech* and by reasoning. As for the previous seed, the two highest associations were with *vision.motion* and *vision.shape* in the ‘perception’ domain.

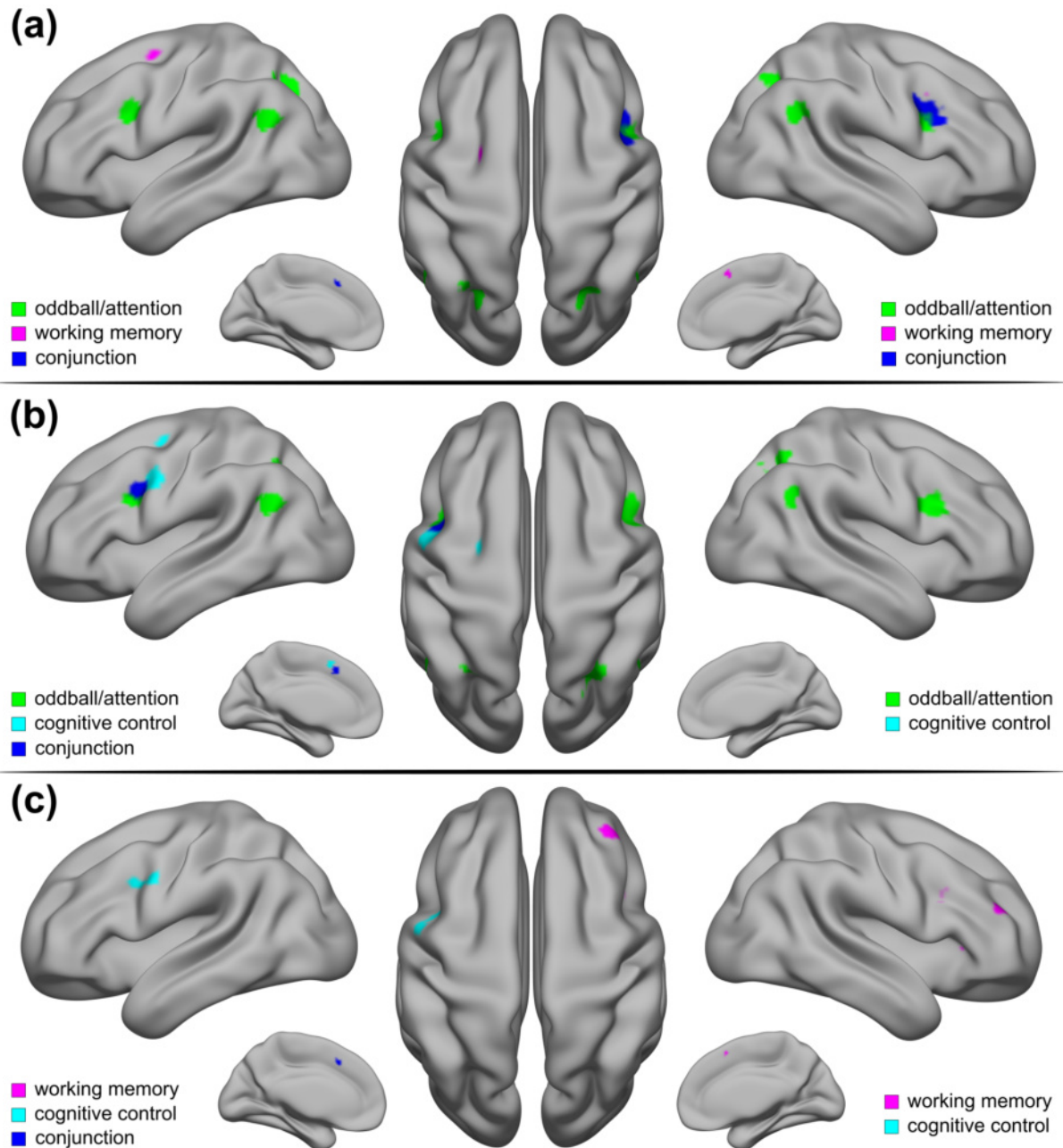


FIGURE S6 Results of the IFJ sample control analysis. The IFJ sample was split into three groups of experiments based on the paradigm employed (oddball/attention, working memory and cognitive control) to explore potential dissociations between them near the IFJ. In line with this possibility, we found a lateralized cluster involved in cognitive control (i.e., task-switching/Stroop paradigms) in the left hemisphere, and a cluster involved in working memory (mainly n-back contrasts) in the right hemisphere. These clusters overlapped with a bilateral cluster associated with oddball/attention experiments at the iPCS and IFS junction, including the IFJ. The oddball/attention clusters were however generally anterior and ventral relative to their location in both hemispheres (see **A** and **B**)

The functional decoding of the LH and RH IFJ coactivation patterns uncovered associations with similar behavioral domains, although with some interesting differences in their predominance. The LH IFJ coactivations had the highest association with attention in the ‘cognition’ domain (see Figure 5, right side of panel C), followed by language.semantics, working memory, and language.speech. The next strongest association was in the ‘emotion’ domain with positive.reward/gain. Then, there were significant associations in the ‘perception’ domain with vision.shape and vision.unspecified and audition. Finally, in the ‘action’ domain we found the most prevalent associations with inhibition and execution.unspecified. As for the previous seed, the RH IFJ had the highest association with attention in the ‘cognition’ domain (see Figure 5, right side of panel D). In the same domain, there were also strong associations with working memory, language.semantics, reasoning, and language.speech. Next, we found two prominent associations in the ‘action’ domain with inhibition and execution.unspecified. Again, we found an association with positive.reward/gain in the ‘emotion’ domain. Lastly, the strongest associations in the ‘perception’ domain were with vision.shape, audition and somesthesis.pain.

3.6.9 | Limitations

While we believe that the present study significantly advances our understanding of the localization and spatial organization of areas in the posterior-lateral PFC, we would like to acknowledge its limitations. First of all, even though the inclusion of ROI analyses is not recommended according to the best practices reported in Muller et al. (2018), we nevertheless decided to include them to increase our sample size, as we were mainly interested in inferring the localization of their peaks. When we excluded them in a control analysis (reported in section 4 above), we showed that the inferred ALE remained virtually identical. We note however that the inclusion of these studies may have inflated the ALE values associated with the FEF and IFJ clusters in our main results, and potentially also their spatial extent. A second limitation of our study is that although we strived to include as many functional localizers as possible, particularly in the IFJ sample many of the included coordinates were only based on the results of the main fMRI task, and not an independent fMRI localizer. It is not clear to what extent these IFJ activations can be replicated, and there may be a file drawer problem in this sample, which is typically an issue in ALE meta-analyses (Acar et al. 2018). A related limitation of our study is the fact that our samples were retrieved by using these regions’ labels from the literature, which may raise a circularity concern. We would like to point out first that these keywords applied to all the fields in the Web of Science and were indexing relevant papers based on any of the three words (e.g., ‘frontal’, ‘inferior’, ‘eye field’, and so on), making these filters much broader than the exact labels. Second, we deem the possibility that, for example, a study investigating oculomotor control using a functional localizer did not report activity in the FEF or cite any related literature on the FEF very unlikely. In the case of the IFJ however, we recognize that this strategy may have introduced some level of bias for studies that used novel fMRI paradigms, which may have been avoided by adopting a more conventional approach, where studies are included mainly according to the type of task employed. Finally, despite the fact that we tried to include experiments that tapped onto similar cognitive functions (i.e., spatial attention and oculomotor control for the

FEF, and attention, working memory and cognitive control for the IFJ) to infer spatial convergence within FEF and IFJ, these experiments didn't measure a single cognitive function but rather a collection of several distinct functions and sub-processes, some of which share an important degree of overlap. The detailed investigation of each separate component of these functions/processes, which are often subsumed under the umbrella term of executive functions, would require examining a broader number of paradigms than we included in our analyses, and could lead to further insights into anatomo-functional dissociations in the prefrontal cortex.

Chapter 4

Surface-based probabilistic tractography uncovers segregated white matter pathways underlying spatial vs non-spatial control

Parts of this work were published as a conference proceeding and as an extended abstract in these Journal issues:

Bedini, M., Olivetti, E., Avesani, P., & Baldauf, D. (2022). The structural connectivity fingerprints of the frontal eye field and the inferior frontal junction. *Journal of Vision*, 22(14), 3280. <https://doi.org/10.1167/jov.22.14.3280>

Bedini, M.; Olivetti, E.; Avesani, P.; Baldauf, D. (2021). TALKS: Submission 84 The anatomical pathways underlying spatial versus non-spatial attention. *Cognitive Processing*, 22, 1–2. <https://doi.org/10.1007/s10339-021-01058-x>

4.1 | INTRODUCTION

A longstanding tradition in contemporary neuroscience argues that in primates, the locus of behavioral control and flexibility is seated in the prefrontal cortex (PFC; Chafee & Heilbronner, 2022; Fuster, 2001; Luria, 1966; Szczepanski & Knight, 2014). Here, several regions constitute crucial hubs that are part of different brain networks with adaptive functions (Assem et al., 2020; Cole et al., 2013; Duncan, 2001; Vincent et al., 2008; Yeo et al., 2011). In this regard, the role of persistent activity within the PFC is widely recognized as the neural substrate of the cognitive processes underlying complex, goal-driven behavior (Curtis & Sprague, 2021; Goldman-Rakic, 1996; Miller & Cohen, 2001; Serences, 2016). In the human posterior-lateral PFC (plPFC), the frontal eye field (FEF; Corbetta & Shulman, 2002; Petit & Pouget, 2019; Vernet et al., 2014) and the inferior frontal junction (IFJ; Brass et al., 2005; Muhle-Karbe et al., 2016) exhibit the characteristics of control regions that are involved in a wide array of processes ranging from attention, working memory, and other forms of cognitive control. Both regions show sustained responses during the cue and delay period of attention and working memory tasks (Astafiev et al., 2003; Courtney et al., 1998; Giesbrecht et al., 2003; Liu et al., 2003; Serences et al., 2004; Zanto et al., 2010) and are involved in biasing activity in posterior brain regions (Baldauf & Desimone, 2014; Barceló et al., 2000; Marshall et al., 2015b; Ruff et al., 2006; Sneve et al., 2013; Veniero et al., 2021; Zanto et al., 2011; Zhang et al., 2018). Crucially, however, recent evidence suggests that they differ in their selectivity to spatial versus non-spatial information: on the one hand, the FEF predominantly encodes spatial information (Fiebelkorn & Kastner, 2020; Jerde et al., 2012; Kastner et al., 2007; Mackey et al., 2017; Sprague & Serences, 2013), whereas, on the other hand, the IFJ may predominantly encode non-spatial (i.e., feature- and object-based) information (Baldauf & Desimone, 2014; Liu, 2016; Liu et al., 2011; O'Reilly, 2010; Zanto et al., 2010). fMRI studies that employed multivariate pattern analysis (MVPA; Haxby, 2012; Kamitani & Tong, 2005) to decode the attended and memorized information from these regions provide some evidence that supports this view (Gong & Liu, 2020; Jerde et al., 2012; Liu, 2016; Liu et al., 2011; Liu & Hou, 2013; Meyyappan et al., 2021; Muhle-Karbe et al., 2017; see chapter 2 for a discussion), albeit none of these studies was able to show a double dissociation in these patterns in the strict sense, which remains a goal for future research. The hypothesis of a dissociation in the selectivity of the FEF and IFJ is strikingly in line with the conceptual framework that was originally proposed by Goldman-Rakic and colleagues (Goldman-Rakic, 1996; Wilson et al., 1993; Constantinidis & Qi, 2018, for a review) to explain the organization of the lateral PFC in non-human primates, based on the evidence from molecular, single-unit recordings, and tract-tracing studies (Cavada & Goldman-Rakic, 1989; Goldman-Rakic, 1996; Funahashi et al., 1989). Concerning the latter research line, tract-tracing evidence suggests that the dorso-lateral PFC and the ventro-lateral PFC are characterized by divergent patterns of anatomical connectivity to the 'what' and 'where' visual pathways (Goodale & Milner, 1992; Mishkin et al., 1983), respectively (Barbas & Pandya, 1989; Felleman & Van Essen, 1991; Webster et al., 1994; Yeterian et al., 2012). In humans, however, the anatomical connectivity of the plPFC remains elusive and is primarily

inferred non-invasively using diffusion MRI (dMRI; Johansen-Berg & Behrens, 2013) and tractography (Jbabdi & Johansen-Berg, 2011; Jeurissen et al., 2019).

Previous dMRI studies were able to reveal that many aspects of the organization of prefrontal connectivity are preserved across the macaque and the human brain (Crosson et al., 2005; de Schotten et al., 2012; Jbabdi et al., 2013a), which allows for the detailed study and identification of potential homologies between the two species (Neubert et al., 2014; Sallet et al., 2013), and crucially to formulate hypotheses motivated by comparative evidence in humans (Mars et al., 2021; Schall et al., 2020). The characteristic patterns of connectivity (i.e., the connectivity fingerprint) of each region in the PFC fundamentally underlies its specialized role in cognition (Mars et al., 2018a; Passingham et al., 2002). Each region's unique set of afferent and efferent connections in fact ultimately constrain the inputs it receives (and consequently its selectivity for specific sensory information), as well as its ability to control and bias activity elsewhere in the brain to solve specific tasks, respectively (Passingham & Lau, 2022; Petrides et al., 2012). Previous dMRI studies were mainly aiming at addressing comparative questions about the organization of the PFC and also to provide a validation of tractography methods by comparing invasive tract-tracing measures with probabilistic tractography results (see for example Jbabdi et al., 2013a). A critical issue of these studies is however that the seed regions used to perform the probabilistic tractography analysis were not functionally localized at the individual subject level. The regions employed were instead derived from atlases based on cytoarchitectonic criteria, thus making it unclear to interpret whether and how the modeled connectivity fingerprints may constrain and underlie the function of the PFC regions examined. In contrast, dMRI studies combining the functional localization of the FEF and IFJ at the individual subject level using fMRI, with the analysis of their structural connectivity with tractography, do offer some interesting preliminary evidence on the involvement of long-range association pathways in mediating the complex goal-driven behaviors associated with these regions (reviewed in chapter 2). Of importance to the present study, the studies by Anderson et al. (2012), Szczepanski et al. (2013), and Umarova et al. (2010) all showed converging evidence that the FEF is wired through fiber pathways running dorsally to the posterior parietal cortex (PPC). Baldauf and Desimone (2014) classified the structural connectivity likelihood of the fusiform face area (FFA) and parahippocampal place area (PPA) seeds (which were defined through an fMRI functional localizer) with the frontal cortex, highlighting the highest probability in regions of the ventro-lateral PFC (including the IFJ). Collectively, these studies were important in suggesting the idea that the PFC communicates with the parietal and temporal cortices through distinct, reciprocal and partially segregated white matter pathways. These putative pathways are moreover known to be supported by specific white matter association fibers (de Schotten et al., 2011). Using an approach known as virtual dissection (Catani et al., 2002), it is possible to delineate fibers that compose large bundles non-invasively via dMRI tractography (Catani & de Schotten, 2008; Warrington et al., 2020). Influential dMRI studies suggest that the major white matter bundle that mediates the communication within the frontoparietal network is the superior longitudinal fasciculus (SLF; de Schotten et al., 2011; Schmahmann & Pandya, 2006), which is subdivided into three branches (SLF1, SLF2, SLF3) that run parallel to each other from the most dorso-medial to the ventro-lateral direction.

Collectively, the SLF is thought to subserve visuo-spatial and attentional functions (de Schotten et al., 2011; Marshall et al., 2015a; Parlatini et al., 2017; Quentin et al., 2015). Indeed, damage to the SLF often leads to the neglect syndrome (Bourgeois et al., 2015; de Schotten et al., 2011; Doricchi et al., 2008), particularly when the right hemisphere is affected (see Bartolomeo & Seidel Malkinson, 2019, for a review). In addition to lesion evidence, which relates specific symptoms to behavioral deficits, the functions of the SLF have also been inferred by combining tractography with meta-analytic techniques. According to a large-scale study combining the virtual dissection of the three branches of the SLF in 129 participants with 14 fMRI meta-analyses, the SLF1 would primarily mediate ‘spatial-motor’ and the SLF3 ‘non-spatial-motor’ cognitive components (Parlatini et al., 2017).

In a more recent and comprehensive effort to understand the organization of the networks involved in attention control in humans, the study by Sani and colleagues (2021) analyzed dMRI data from 263 participants released by the Human Connectome Project (HCP; Van Essen et al., 2013) using constrained spherical deconvolution (Tournier et al., 2007) and probabilistic ensemble tractography (Takemura et al., 2016). Their study provided compelling evidence that the putative human posterior infero-temporal area (phPIT) forms part of an interconnected network encompassing the FEF and the lateral intraparietal area dorsal (LIPd) as defined by the multi-modal parcellation (MMP1) by Glasser et al. (2016). The FEF and LIPd are two areas well known to be involved in the control of spatial attention and form the core of the dorsal attention network (Corbetta & Shulman, 2002; Fiebelkorn & Kastner, 2020). The additional involvement of the area phPIT was revealed using fMRI in a motion discrimination attentional task, complemented by two additional functional localizers and retinotopic mapping to better refine its boundaries relative to nearby visual regions. Finally, this study also uncovered the white matter bundles underlying the connectivity patterns found in the whole-brain connectome by using waypoint masks and computing their spatial overlap with an independent bundle segmentation (Bullock et al., 2019). Using this method, the authors showed that the communication between FEF and LIPd is mediated by the SLF2 and in part by the SLF3, that between FEF and phPIT by the posterior branch of the arcuate fasciculus (AF) and the temporo-parietal connection to the superior parietal lobule (SPL), and finally that between LIPd and phPIT by the AF and the inferior fronto-occipital fasciculus (IFOF). The evidence for the latter two connections (in terms of spatial overlap and streamline endpoints) however wasn’t exactly clear, which suggests that these connections may be not well characterized by current models of bundle organization. Interestingly, the organization of the frontoparietal bundles (i.e., the FEF-LIPd connections) matches well the one described in their previous study in the macaque using the same non-invasive techniques (i.e., dMRI, fMRI attentional localizer task; Sani et al., 2019). In summary, this study highlights the complex organization of the attention networks across three lobes of the human cerebral cortex.

Overall, the studies discussed in the previous paragraphs provide valuable evidence to understand the organization of the connectivity within the attention (i.e., dorsal and ventral attention network; DAN, VAN, respectively) and frontoparietal (FPN) networks, which may

help clarify the specific functional role of each of their nodes. We note however that these studies arguably face a tradeoff between having limited statistical power (Botvinik-Nezer et al., 2020; Button et al., 2013), but with the great advantage of having seeds functionally localized at the individual level, as opposed to the ability to perform analyses on very large datasets but with regions defined at the group level (i.e., using an atlas), which may however not represent the individual brain organization faithfully. Even though the functional localization of ROIs at the individual level seems to be to date the most accurate way to overcome the issues associated with group-level analyses performed on a brain template (Coalson et al., 2018; Fedorenko, 2021) and crucially to infer their connectivity fingerprints and interpret them in a way that bears a strong relationship with their function (Mars et al., 2018a), the localization of the seeds regions may, in fact, be difficult and impractical to scale to larger samples. As a consequence of the former limitation, another major barrier in adequately mapping the connectivity fingerprints of a brain region is the fact that most available models of brain organization (i.e., brain atlases and parcellations, which are often used as surrogates of the localization of brain regions based on functional localizers) aren't tailored to incorporate information from large collections of task-fMRI data (Eickhoff et al., 2018b; but see Fan et al., 2016, and Glasser et al., 2016). Indeed, as I argued in chapter 3 there may be important discrepancies between the localization of regions in the PFC as inferred from task-based fMRI and the MMP1. In the activation likelihood estimation (ALE) fMRI meta-analysis presented in that chapter, I attempted to overcome these issues by modeling the average localization of FEF and IFJ in standard space using two samples of experiments from well-replicated fMRI paradigms that target these regions. This meta-analytic technique allows to infer robust brain-behavior relationships and to model spatial uncertainty related to inter-individual variability (Eickhoff et al., 2012). Using the coordinates inferred from a meta-analysis has the advantage of enabling us to relate the functional specialization of FEF and IFJ to their underlying connectivity patterns in large neuroimaging datasets. Although previous tractography studies suggest that the FEF and the IFJ may communicate with posterior parietal and temporal regions through different and segregated pathways (Anderson et al., 2011; Baldauf & Desimone, 2014; de Schotten et al., 2011; Sani et al., 2021; Szczepanski et al., 2013; Umarova et al., 2010), no study has yet directly contrasted their connectivity fingerprints to the dorsal and ventral visual streams (Goodale & Milner, 1992; Mishkin et al., 1983). A divergence in these patterns would be expected based on the principles of anatomical connectivity discovered in the macaque PFC (Cavada & Goldman-Rakic, 1989; Romanski, 2004; Webster et al., 1994; Yeterian et al., 2012), and may help to further highlight how long-range association pathways underlie the functional specialization of these regions in spatial versus non-spatial control processes. Therefore in the present study, we sought to investigate the structural connectivity fingerprints of the FEF and IFJ with posterior visual regions. In particular, we combined an ALE meta-analysis - which allowed us to accurately infer the localization of these regions in standard space - with surface-based probabilistic tractography (Hernandez-Fernandez et al., 2019) - to contrast their connectivity likelihood to the global dorsal and ventral visual streams (Goodale & Milner, 1992). Finally, we also performed the virtual dissection of the major white matter association bundles connecting the PFC and posterior regions to further uncover

the structures underlying the connectivity patterns hypothesized (Barrett et al., 2020; Warrington et al., 2020).

4.2 | MATERIALS AND METHODS

4.2.1 Subjects and data sources

In the present study, we used the structural and dMRI data from the HCP MEG subjects release (Van Essen et al., 2013), which is publicly available at: <https://db.humanconnectome.org>. Thanks to the access to restricted demographic information, we retrieved a subset of the data by filtering the initial sample ($n = 95$) according to the following criteria (see Figure 1 for a schematic): first, we discarded subjects who had documented quality control issues ($n = 4$); next, we identified all the subjects with family relationships (i.e., twins), and a single twin was randomly selected while all the related twins were discarded from the sample. This led to the inclusion of 36 subjects with no family relationship. Finally, we added to this sample all the unrelated subjects from the release who also had resting-state MEG data available ($n = 20$), since the parallel analysis of the latter modality is part of ongoing work from our lab. Hence, for all the analyses reported in the following, our sample is composed of a total of 56 subjects from the HCP MEG release (age range: 22-35, mean = 28.66 ± 3.81). This sample size is considerably larger compared to previous dMRI studies (see the Introduction section) and is crucial to enable reliable statistical inference for dMRI tractography, whose results are still in need of being validated more thoroughly by comparing them with *ex-vivo* data (see Donahue et al., 2016; Grisot et al., 2021; Miller et al., 2011; Reveley et al., 2015; Sarwar et al., 2021; Van den Heuvel et al., 2015).

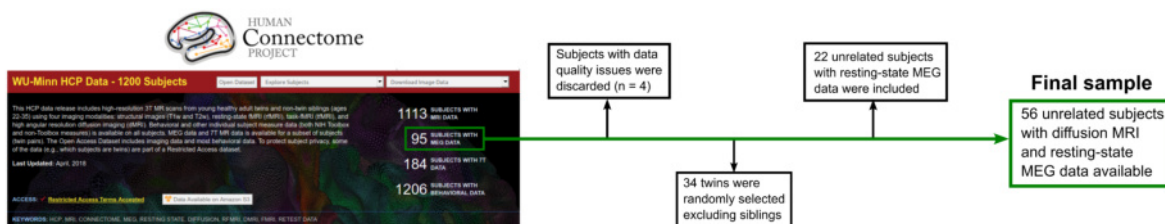


FIGURE 1 Schematic of the sample selection procedure from the HCP-MEG dataset.

4.2.2 Localization of the FEF and IFJ seed regions

We performed an ALE fMRI meta-analysis (Eickhoff et al., 2012) to infer the most accurate localization of the FEF and IFJ in MNI152 space. This analysis was carried out on subsamples of the list of studies presented in chapter 3 of this dissertation. In the FEF subsample, we included all the tasks that were analyzed in chapter 3 (i.e., prosaccades > fixation, antisaccades > fixation and antisaccades > prosaccades, valid > neutral/invalid trials), with the addition of more complex oculomotor contrasts (for examples, see Jarvstad & Gilchrist, 2019, and Thakkar et al., 2014). In contrast, in the IFJ subsample, we included all

the studies presented in chapter 3 with the exception of Meyyappan et al., (2021). Both subsamples included 21 studies from which a single contrast of interest was used as input for ALE (see Appendix A, Tables 1 and 2 for details about the FEF and IFJ studies, respectively). There were 25 experiments in the FEF sample and 22 experiments in the IFJ sample. Thus, despite the fact that our samples were lower than the analysis presented in chapter 3, this analysis was still adequately powered according to the recommendations by Eickhoff et al. (2016), who recommend 17-20 experiments as a lower boundary. The ALE parameters were set to $p = 0.01$ and a cluster-level family-wise error (FWE) = 0.01 using 1000 permutations. Given these differences in the two meta-analyses samples, the coordinates of the ALE peaks generally matched but were slightly shifted in the case of RH FEF (here LH FEF: -28, -6, 54, and RH FEF: 32, -4, 52, whereas in chapter 3 they were LH FEF: -28, -6, 54, and RH FEF: 30, -6, 50), and LH IFJ (LH IFJ: -42, 8, 26, and RH IFJ: 46, 12, 28, whereas in chapter 3 they were LH IFJ: -42, 6, 30, and RH IFJ: 46, 12, 28), although they remained identical for the LH FEF and the RH IFJ. To the extent that our method allowed, these differences should only have minor effects on the results presented in the following as our seeding approach included the updated ALE peak coordinates corresponding to the results from our larger ALE meta-analysis presented in chapter 3. We refer to section 4.2.4 for additional details about our seeding approach.

4.2.3 Probabilistic tractography method

The analyses of dMRI data were performed using the FSL FDT software (Jenkinson et al., 2012; v. 6.0.5). We downloaded the preprocessed 3T dMRI data of the 56 subjects selected from: <https://db.humanconnectome.org>. The HCP 3T dMRI was acquired at multiple b-values ($b = 1000, 2000, \text{ and } 3000 \text{ s/mm}^2$) and by sampling 90 directions for each shell, with 1.25mm isotropic resolution. Importantly, this acquisition scheme was allowed by the use of a customized 3T (Siemens Skyra) ‘Connectome’ scanner with increased gradient strength (100 mT/m) and multiband pulse sequences (Elam et al., 2021). The HCP consortium developed and improved a preprocessing pipeline to compensate for the increased distortions in the data due to their custom acquisition (Sotiropoulos et al., 2013a). Susceptibility-induced distortions, eddy currents and subject motion were corrected using tools from FSL (namely, topup and eddy; Anderson & Sotiropoulos, 2016). Collectively, the efforts from HCP to optimize data acquisition, increasing spatial resolution, and their careful preprocessing approach led their consortium to release dMRI data of unparalleled quality (Elam et al., 2021). This high spatial resolution and excellent data quality across modalities (MRI, dMRI) is particularly beneficial for the aims of our study, as mitigating partial volume effects (i.e., the mixing of different tissue types within a voxel; Miller et al., 2011) can help achieve better accuracy in assigning streamlines to their targets when tracking near the cortex (Hernandez-Fernandez et al., 2019; Sotiropoulos et al., 2013a). All the dMRI analyses reported in the following were performed on the subjects’ native space in the original data resolution (i.e., 1.25mm). First, we ran the FSL command DTIFIT on the preprocessed dMRI data to obtain the fractional anisotropy (FA) image, which we used for performing image registrations to the native dMRI space from the FreeSurfer space. The HCP extended structural preprocessing folder contains all the outputs from the FreeSurfer recon-all

segmentation pipeline, including the pial and white matter surfaces. To infer the connectivity likelihoods between our seed and target regions, we implemented the FSL FDT analysis pipeline, which involves two main steps, namely `bedpostx` (Jbabdi et al., 2012) and `probtrackx` (Behrens et al., 2007). `Bedpostx` is a Bayesian approach for estimating the fiber orientation distribution function (fODF) using Markov Chain Monte Carlo methods (Behrens et al., 2003). `BedpostX` models the diffusion signal in each voxel with 2 compartments, which is commonly referred to as the ‘ball and stick’ model (Jbabdi et al., 2012). Importantly, this method allows the modeling of up to 3 fiber orientations in each voxel (Behrens et al., 2007). An automatic relevance determination algorithm prunes exceeding fibers that are not supported by evidence from the data (Behrens et al., 2007). An additional iteration of `bedpostx` involves the modeling of non-monoexponential signal decays in multi-shell data (Jbabdi et al., 2012), which is currently what is implemented as model 2 in the FSL version we used. Recent progress in the analysis of multi-shell dMRI data led to the development of `Rubix` (Sotiropoulos et al., 2016), which is an improved data fusion approach suitable for 3T and 7T HCP data. Due to its high computational demands, `Rubix` was run by adapting the GPU version of `bedpostx` implemented on a CUDA architecture (Hernández et al., 2013) and the 3T dMRI processed data was released by the HCP in December 2016. Given that this step is computationally intensive and the advantages offered by the GPU implementation of `bedpostx` (Sotiropoulos et al., 2016), we downloaded the processed 3T dMRI HCP data (i.e., the `bedpostx` outputs) of the 56 subjects selected and used them as starting points for our probabilistic tractography pipeline. The following sections describe in detail our methodology for `probtrackx` (Behrens et al., 2007).

4.2.4 Seeding approach and motivation

The FEF and IFJ seeds were mapped to the native dMRI space using the FNIRT warp files present in the HCP 3T structural MRI directory by applying these transformations to the ALE FEF and IFJ peak coordinates in MNI152 space and using the FA image as a reference. The ALE peaks of each seed were then projected onto the WM/GM boundary of each subject’s (the low-resolution native white matter surface, i.e., with 32k vertices) as follows. We first created a sphere of a 2.5mm radius centered around the ALE peak non-linearly registered to the native diffusion space. Each FEF and IFJ sphere therefore consisted of a 6.25mm diameter sphere at this stage. We note that by virtue of this method our spheres now also included the coordinates corresponding to the ALE peaks presented in chapter 3. Next, we used the command-line tool `surf_proj` from FSL to map these spheres to the white matter/grey matter (WM/GM) boundary as provided by the FreeSurfer segmentation (i.e., `*h_white.gii`). The latter file was mapped from the FreeSurfer space to the diffusion space using the tool `surf2surf` from FSL as described in the wiki (<https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FDT/UserGuide>). We used the ‘mean’ method in `surf_proj`, and we further increased the step size by the voxel size (i.e., 1.25mm) until each subject had identifiable vertices corresponding to the volumetric spheres (see Figure 2 for examples of this projection). For all the subjects analyzed, the final step size was set to 2.5mm. We note that this value roughly matches the cortical thickness observed in the regions

lying next to the superior precentral sulcus (sPCS) and inferior precentral sulcus (iPCS; Glasser et al., 2016).

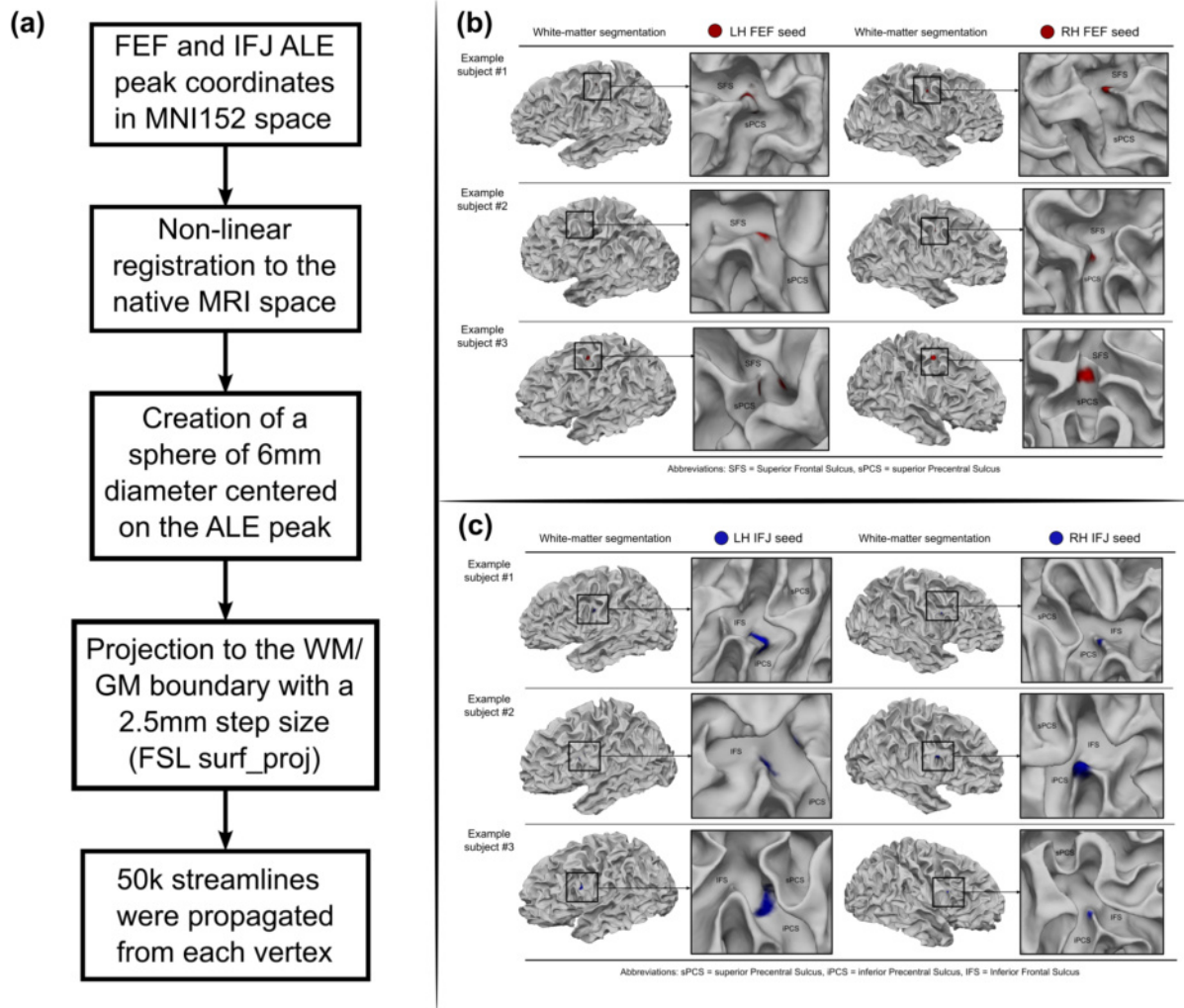


FIGURE 2 A Projection to the WM/GM boundary method and examples for the B the FEF seed projections and C the IFJ seed projections.

4.2.5 Cortical parcellation and definition of the target regions of the two visual streams

Recent approaches to parcel the human cortex can leverage multiple sources of information (Eickhoff et al., 2018b), including structural, functional and connectional information. In this regard, the MMP1 published by Glasser et al. (2016) represents a step change in our understanding of the macro-organization of the human cortex based on the combination in architecture, function, retinotopy and connectivity as measured from 210 individuals using high-resolution data acquired with the HCP protocols. By detecting sharp changes across these features, Glasser et al. (2016) delineated the boundaries of a total of 180 regions per hemisphere, providing one of the most detailed atlases available to date. This atlas arguably provides us with unique advantages to systematically investigate the connectivity of FEF and IFJ to the posterior visual cortex defined using these multimodal

criteria. The MMP1 was projected on Fsaverage (Fischl et al., 1999) following the indications from Coalson et al. (2018) by Mills (2016) and was publicly made available at https://figshare.com/articles/dataset/HCP- MMP1_0_projected_on_fsaverage/3498446. The resulting FreeSurfer annotation files from the MMP1 atlas were mapped to the native structural space using the script developed by the CJ Neurolab ([https://figshare.com/articles/dataset/HCP-MMP1_0_volumetric NIfTI_masks_in_native_structural_space/4249400](https://figshare.com/articles/dataset/HCP-MMP1_0_volumetric_NIfTI_masks_in_native_structural_space/4249400)), which is based on spherical landmark registration (with the FreeSurfer command `mri_label2label`; FreeSurfer v6.0; Fischl et al., 1999). In brief, this script converted these annotation files to label files and mapped them to the native subject space using the FreeSurfer command `mri_label2label`. After these steps, all the labels from the atlas were registered onto the WM/GM boundary of each subject's (the low-resolution white matter surface, i.e., with 32k vertices) as estimated by the FreeSurfer reconstruction (based on the extensive preprocessed structural data resulting from HCP pipelines) using the FSL's command `label2surf`. It is important here to highlight the fact that these surface-based registration methods achieve much better consistency in labeling cortical areas and better capture intersubject variability compared to traditional volumetric methods (e.g., FSL's FNIRT; Coalson et al., 2018). More specifically, according to Coalson et al. (2018), the MMP1 can be adequately mapped by using multimodal surface matching (MSM; Robinson et al., 2014) and FreeSurfer registration algorithms, while FNIRT has the worst performance in capturing interareal variability compared to the former two (Coalson et al., 2018). Their study shows that FreeSurfer registration is able to capture 0.473 of the surface area, while 'MSMAll', and FNIRT capture 0.564 and 0.367, respectively. Therefore, by using the procedure described above to map the MMP1 parcellation to the native dMRI space, we were able to achieve high fidelity in mapping this atlas to the individual cortical anatomy.

To select the parcels of the MMP1 atlas that belonged to the dorsal and ventral visual streams, I carried out a literature review that included comparative and human fMRI evidence (Goodale & Milner, 1992; Kravitz et al., 2011, 2013; Wang et al., 2015; Zimmermann et al., 2018) and was guided by the accompanying materials from the original atlas publication (see Glasser et al., 2016, supplementary information #3). We note that a previous study already investigated the connectivity of the extrastriate body area with the dorsal and ventral visual streams as defined by the MMP1 atlas (Zimmermann et al., 2018). In contrast to this study, since our study did not involve confounds due to the proximity of the targets to the seed regions, we could include additional parcels from the MMP1 that were discarded by the authors for this reason. In addition, we took into account another defining characteristic of the dorsal visual stream, namely the presence of topographic visual organization, to better refine the inclusion criteria for the parcels belonging to this stream. To assess whether a parcel could be considered topographically organized, we visualized both the MMP1 and the atlas by Wang et al. (2015) by overlaying them on FSaverage (Fischl et al., 1999). In particular, I visualized the maximum probability maps from Wang's atlas and hypothesized a one-to-one correspondence between their regions. Even though these studies relied on different data sources to create their parcellations, it is widely assumed that the different cortical features have a high degree of alignment (Glasser et al., 2016) especially early in the visual hierarchy

(for example, topography and myelin content; see Abdollahi et al., 2014). Therefore, I expected to find a similar arrangement of regions between the two atlases, which was confirmed qualitatively by visual inspection. Finally, we excluded from our visual streams' definition parcels nearby the medial wall, and parcels from the superior temporal lobe and the temporo-parietal junction were also excluded since they are likely characterized by distinctive connectional profiles (Kravitz et al., 2013; Mars et al., 2011). In Table 1, I list the MMP1 parcels that we included in the definitions of dorsal and ventral visual streams. Crucially, we also decided to not include early visual regions in our probabilistic tractography analysis, for several reasons. Even though prominent models suggest for example reliable functional interactions between FEF and V4, especially in the macaque model (Buschman & Miller, 2007; Moore & Armstrong, 2003), it is unclear whether similar effects are direct or indirect in humans (Kastner & Ungerleider, 2000). Furthermore, there is also converging fMRI and EEG evidence of interactions between IFJ and V4 (Zanto et al., 2010, 2011; Zhang et al., 2018), which however again leaves open the question of whether these effects are direct or indirect. Another motivation relates to the fact that all the early visual regions are topographically organized (Sereni et al., 1995; Wang et al., 2015), while some display spatial and feature selectivity (Maunsell, 2015), hence potentially constituting a zone of graded influence from either the FEF or the IFJ. In summary, based on these arguments, we decided to exclude early visual cortex regions from our analyses.

4.2.6 Surface-based probabilistic tractography with GPU acceleration

The multi-shell dMRI data from the HCP allows to take advantage of the better sensitivity in detecting fiber crossing and conveniently model them using bedpostx (Jbabdi et al., 2012). Probtrackx samples the fiber orientation estimated with bedpostx to generate a connectivity distribution between user-defined seed and target regions (Behrens et al., 2007). This algorithm involves three steps: the first randomly samples a fiber orientation from a voxel, the second is to propagate along the sampled fiber direction for a fixed distance, and finally the third step checks for any termination criteria for streamline propagation (Behrens et al., 2003). Importantly, probtrackx estimates how robust the connection is against noise and uncertainty, or in other words how reproducible it is (Jbabdi & Johansen-Berg, 2011). This method thus allows us to infer how likely it is that a region is on the dominant pathway of anatomical connectivity from a seed region (Jeurissen et al., 2019). Overall, our general approach for probabilistic tractography closely follows the one published in Donahue et al., (2016), and in particular, the approach for the generation of their dense connectome matrix (termed dDT1 in that publication). We chose to follow this cortical tracking approach as their study showed that it improved the agreement between dMRI derived connectivity from probtrackx and retrograde tracing in the macaque, with a correlation factor of $r = 0.59$. In contrast to their study however, our tracking approach results are stored in a parcellated connectome based on the MMP1 atlas without further data processing. As done in that study, we also tracked the streamlines ipsilaterally from each hemisphere (Donahue et al., 2016).

Table 1 List of the parcels for the confirmatory classification targets analysis

Parcel	Stream	Full name	Parcel	Stream	Full name
V3A	Dorsal	Area V3A	V8	Ventral	Eight Visual Area
V3B	Dorsal	Area V3B	VVC	Ventral	Ventral Visual Complex
V6	Dorsal	Sixth Visual Area	PIT	Ventral	Posterior InferoTemporal
V6A	Dorsal	Area V6A	FFC	Ventral	Fusiform Face Complex
V7	Dorsal	Seventh Visual Area	VMV1	Ventral	VentroMedial Visual Area 1
IPS1	Dorsal	IntraParietal	VMV2	Ventral	VentroMedial Visual Area 2
7AL	Dorsal	Lateral Area 7A	VMV3	Ventral	VentroMedial Visual Area 3
7PL	Dorsal	Lateral Area 7P	TE1a	Ventral	Area TE1 anterior
7PC	Dorsal	Area 7PC	TE1m	Ventral	Area TE1 middle
LIPd	Dorsal	Area Lateral IntraParietal dorsal	TE1p	Ventral	Area TE1 posterior
LIPv	Dorsal	Area Lateral IntraParietal ventral	TE2a	Ventral	Area TE2 anterior
VIP	Dorsal	Ventral IntraParietal Complex	TE2p	Ventral	Area TE2 posterior
MIP	Dorsal	Medial IntraParietal Area	TF	Ventral	Area TF
IP1	Dorsal	Area IntraParietal 1	PHT	Ventral	Area PHT
V3CD	Dorsal	Area V3CD	PH	Ventral	Area PH
LO3	Dorsal	Area Lateral Occipital 3	TGv	Ventral	Area TG ventral
MT	Dorsal	Middle Temporal Area			

Probtrackx was performed by leveraging the GPU implementation of this tool developed by Hernandez-Fernandez et al. (2019) on a CUDA 9.2 parallel architecture. To perform this step, we split up the list of targets into 4 sub-groups due to the exceedingly large memory demands of the computations. The analysis was implemented by setting the following probtrackx parameters: 50000 streamlines were propagated from each seed vertex for a maximum of 3200 steps using modified Euler integration. The curvature threshold was set to 0.2 (corresponding to an 80° turn) with a step length of 0.3125 mm (1/4 of the voxel length, as in Donahue et al., 2016), and the ‘loopcheck’ flag was enabled to discard artifactual loops of the streamlines. We used the corpus callosum, subcortical nuclei, cerebellum, and cerebrospinal fluid masks resulting from the FreeSurfer segmentation (i.e., the aseg.mgz file) as ‘avoid’ masks. The native pial surface was instead used as a ‘termination’ mask since this approach is effective in preventing invalid jumps of the streamlines between adjacent gyri (Hernandez-Fernandez et al., 2019). Whenever a streamline crossed the WM/GM boundary, the streamline count was increased for the cortical target corresponding to that vertex. Our methodological approach builds on the growing literature that focuses on the problem of assigning streamline terminations to cortical areas (Schilling et al., 2017; St-Onge et al., 2018; Yeh et al., 2019), and the converging evidence suggesting that surfaces are better equipped to handle more complex geometrical configurations that are not easy to resolve using more conventional volumetric analyses (Cottaar et al., 2021; Shastin et al., 2022; Van Essen & Drury, 1997; Yeh et al., 2019). This is because parcellations in volumetric format create a jagged boundary between the white matter and the grey matter, with the result that they incorrectly assign streamline terminations to regions that encroach on the white matter (Yeh et al., 2019). Thus, these structural

connectome reconstructions are much more prone to partial volume effects (Cottaar et al., 2021; Kleinnijenhuis et al., 2015; Parvathaneni et al., 2019; Roine et al., 2014). Moreover, it has been well documented that there is a ‘gyral bias’ in tractography (Cottaar et al., 2021; Kleinnijenhuis et al., 2015; Reveley et al., 2015; Schilling et al., 2017), which refers to the effect where streamlines tend to terminate more frequently on the gyral crowns rather than in the walls or in the fundus of the sulci (Van Essen et al., 2013). This bias particularly affects long-range association fibers (Reveley et al., 2015), such as the ones we aimed to track in our analysis. Several studies have shown that seeding from the WM/GM boundary using a probabilistic algorithm, and using surface files as termination masks (either a pial or mid-thickness surface), as in the approach we have described above, can significantly mitigate this bias (Girard et al., 2014; Schilling et al., 2017; Smith et al., 2012), although it doesn’t entirely eliminate it (Schilling et al., 2017). For the analysis focusing on the distance confounding factor, we repeated the same command as previously described and enabled the ‘pd’ flag in probtrackx, which multiplies the streamline count for each parcel by the average distance traveled by the respective streamlines. This approach can be considered a fairly conservative method to rule out the influence of this bias on the estimated connectivity likelihoods (Hagmann et al., 2008; Roberts et al., 2016).

4.2.7 Post-processing, statistical analysis and data visualization

Because our seeding strategy involves the propagation of the streamlines from a variable number of seed vertices, the total number of streamlines initialized is given by 50000 times the number of vertices. The individual raw streamline counts were summed across vertices and normalized by computing the ratio between the surviving streamline count (SSC) and the total number of streamlines propagated from each seed region that were not rejected based on our avoid masks (W ; also termed waytotal in probtrackx; see Eichert et al., 2020 for a similar approach). The normalized streamline count (NSC) therefore is given by:

$$NSC = \frac{SSC}{W}$$

We decided to not normalize the values according to the size of the targets (as done for example in Baldauf & Desimone, 2014). Although our target regions vary in size and in how they relate to the cortical morphology (i.e., the gyral patterns), and this could partly explain the difference observed in their streamline counts, our focus was on contrasting each target between ipsilateral seeds (i.e., FEF and IFJ), and hence this aspect wasn’t critical in our analysis. However, we recognize that when analyzing the outputs from the single seeds, this factor may play a role in shifting the connectivity weights higher towards larger-sized cortical targets. After these steps, the NSC were averaged across all subjects for each seed to target region pairs. We contrasted each seed (FEF, IFJ) to target (dorsal, ventral) NSC performing paired t -tests with $p = 0.01$ and correcting for multiple comparisons with the false discovery rate (FDR; $q < 0.05$; Benjamini & Hochberg, 1995). We first assessed whether our data was normally distributed via a Shapiro-Wilk test, and whenever this assumption was violated, we implemented our analysis using the Wilcoxon’s signed-rank test. We also performed a control

analysis to account for a potential distance confound by repeating the same statistical contrast (again applying FDR) on the probtrackx outputs that were distance-corrected using the ‘pd’ flag in FSL. The statistical analyses were performed using the JASP software package (JASP Team, 2023). The FDR was computed using the web utility provided by the software Seed-based d Mapping available at: <https://www.sdmproject.com/utilities>. The visualizations of the cortical connectivity values were created using Connectome Workbench (v. 1.5.0; Marcus et al., 2013). Custom code written in MATLAB2019b (MathWorks) was used to generate the RGB values corresponding to the connectivity likelihoods based on the diverging colormaps developed by Brewer (<https://colorbrewer2.org>). The raincloud plots were created using the Python code and functions from: <https://github.com/pog87/PtitPrince> (Allen et al., 2021). Finally, all the NSC were log-2 scaled for visualization convenience. This was necessary as we tracked from a variable number of vertices across subjects, which led to highly non-linear increases in the number of SSC.

4.2.8 Automatic segmentation of the association white matter bundles of the frontal lobe, analysis of bundles’ asymmetries and of the cortical projections of the SLF

In Warrington et al. (2020), the authors systematically developed and validated a method for the automatic segmentation of the major white matter bundles in the HCP and UK-Biobank datasets. In summary, this method leverages user defined waypoints, exclusion and termination masks, and by initializing probtrackx from specific seed masks enables their virtual dissection (Catani & de Schotten, 2008). We used this method to reconstruct the white matter association bundles of the frontal lobe that could potentially overlap with FEF and IFJ ALE clusters using the definitions provided by the study from Barrett et al. (2020). Our bundles of interest included the arcuate fasciculus (AF), the three branches of the superior longitudinal fasciculus (SLF1, SLF2, and SLF3), and the uncinate fasciculus (UF). For this analysis, we used a sub-sample of 24 participants from the same 3T dMRI HCP MEG dataset. This analysis was also performed using the GPU version of probtrackx (Hernandez-Fernandez et al., 2019). All the white matter bundles of interest were segmented in the subjects’ native space. The bundles were normalized by their streamline count, binarized at 0.5%, and a lateralization index (L) was computed using the formula (where V = volume):

$$L = \frac{V_{RH} - V_{LH}}{V_{RH} + V_{LH}}$$

The normality assumption was checked for all bundles with the Shapiro-Wilk test, and we assessed bundle lateralization using one sample *t*-tests ($p = 0.05$) as in de Schotten et al. (2011). This was done to assess potential differences between the two hemispheres that may provide complementary evidence to our surface-based probabilistic tractography analysis. In addition, this provided an indirect way to carry out a sanity check on our bundle segmentation results, as we expected to find results largely in line with the literature on bundle lateralization (for example, the SLF2; de Schotten et al., 2011).

Our method to estimate the cortical projections of the three branches of the SLF involved the following steps (see Figure 8, panel A): first, we mapped the FEF and IFJ ALE clusters in MNI152 space to each subject's T1w image using a non-linear registration with the FNIRT warps estimated by HCP on the structural data. By leveraging the subject specific tissue segmentation, we removed all the voxels of the clusters that were contained within the white matter. We then dilated the ALE masks using a 3x3x3 mm kernel. This step was crucial to allow the clusters to reach the superficial white matter and follows closely similar approaches to estimate the bundle's terminations (Pestilli et al., 2014; Takemura et al., 2016; Sani et al., 2019). To quantify the likelihood of cortical terminations to each ALE cluster, we normalized the streamline count by the number of overlapping voxels between each SLF branch and the FEF and IFJ ALE clusters separately. We contrasted the streamline count projecting to the FEF and IFJ clusters for the SLF1, SLF2, and SLF3 by performing Wilcoxon's signed-rank tests with $p = 0.01$.

4.2.9 Data availability

The structural and diffusion MRI data released by the HCP were downloaded from: <https://db.humanconnectome.org>. The HCP pipelines can be found at: <https://github.com/Washington-University/HCPpipelines>. The command-line tools from the FSL FDT toolbox are available from: <https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSL>. The binaries of probtrackX GPU implementation were downloaded from: https://users.fmrib.ox.ac.uk/~moisesf/Probtrackx_GPU/Installation.html. The code for mapping the MMP1 atlas to the native structural space can be found at: https://figshare.com/articles/dataset/HCP-MMP1_0_volumetric_NifTI_masks_in_native_structural_space/4249400.

4.3 | RESULTS

4.3.1 Surface-based probabilistic tractography results

We contrasted the NSC for each seed to ipsilateral targets separately in each hemisphere (LH, RH) using the Wilcoxon's signed-rank test (w), since in all these contrasts the data violated the normality assumption. All the p values reported are adjusted for multiple comparisons using the FDR ($q < 0.05$). The contrast between the LH FEF and the LH IFJ NSC revealed that in the dorsal visual stream several regions had higher connectivity likelihood with the LH FEF compared to the LH IFJ (see Figure 3; parcels are always listed from the most anterior to posterior): 7PC ($w, p < 0.001, r_B = 0.722$), 7AL ($w, p < 0.001, r_B = 0.9$), LIPd ($w, p < 0.001, r_B = 0.65$), LIPv ($w, p < 0.001, r_B = 0.706$), VIP ($w, p < 0.001, r_B = 0.934$), IP1 ($w, p < 0.001, r_B = 0.843$), MIP ($w, p < 0.001, r_B = 0.872$), 7PL ($w, p < 0.001, r_B = 0.875$), IPS1 ($w, p < 0.001, r_B = 0.924$), V7 ($w, p < 0.001, r_B = 0.648$), V6A ($w, p < 0.001, r_B = 0.703$), V3CD ($w, p < 0.001, r_B = 0.851$), and V3B ($w, p < 0.001, r_B = 0.945$). All the remaining contrasts were not significant. Vice versa, the contrast between the LH FEF and the LH IFJ NSC revealed that in the ventral visual stream several regions had higher connectivity likelihood with the LH IFJ compared to the LH FEF (see Figure 4): TGv ($w, p <$

0.001, $r_B = -0.559$), TE2a ($w, p < 0.001, r_B = -0.657$), TE1m ($w, p = 0.002, r_B = -0.495$), and TE1p ($w, p < 0.001, r_B = -0.739$). The LH FEF had in contrast higher connectivity likelihood with the areas VVC ($w, p = 0.006, r_B = 0.550$) and FFC ($w, p = 0.006, r_B = 0.503$) compared to the LH IFJ. All the remaining contrasts were not significant. The contrast between the RH FEF and the RH IFJ NSC revealed that in the dorsal visual stream, only one region had higher connectivity likelihood with the RH FEF compared to the RH IFJ (see Figure 5), namely 7AL ($w, p = 0.001, r_B = 0.558$). All the remaining contrasts were not significant. Vice versa, the contrast between the RH FEF and the RH IFJ NSC revealed that in the ventral visual stream, several regions had higher connectivity likelihood with the RH IFJ compared to the RH FEF (see Figure 6): TGv ($w, p < 0.001, r_B = -0.877$), TE2a ($w, p < 0.001, r_B = -0.87$), TE1a ($w, p < 0.001, r_B = -0.719$), TF ($w, p < 0.001, r_B = -0.628$), TE1m ($w, p = 0.002, r_B = -0.821$), TE2p ($w, p < 0.001, r_B = -0.62$), TE1p ($w, p < 0.001, r_B = -0.94$), PH ($w, p < 0.001, r_B = -0.772$), and VMV1 ($w, p = 0.009, r_B = -0.853$). All the remaining contrasts were not significant.

In order to better understand these results and replicate them, we investigated whether they could be due to a distance confound between the seed and the target regions. Therefore, we reanalyzed our data using the probtrackx outputs that were corrected by distance and followed the same statistical procedure. In these outputs, each SSC is multiplied by the average length traveled by the streamlines to reach their targets. All the p values reported are adjusted for multiple comparisons using the FDR ($q < 0.05$). The contrast between the LH FEF and the LH IFJ distance-corrected NSC revealed that in the dorsal visual stream, several regions had higher connectivity likelihood with the LH FEF compared to the LH IFJ: 7PC ($w, p < 0.001, r_B = 0.685$), 7AL ($w, p < 0.001, r_B = 0.901$), LIPd ($w, p < 0.001, r_B = 0.658$), LIPv ($w, p < 0.001, r_B = 0.64$), VIP ($w, p < 0.001, r_B = 0.904$), IP1 ($w, p < 0.001, r_B = 0.835$), MIP ($w, p < 0.001, r_B = 0.857$), 7PL ($w, p < 0.001, r_B = 0.872$), IPS1 ($w, p < 0.001, r_B = 0.847$), V7 ($w, p < 0.001, r_B = 0.825$), V6A ($w, p < 0.001, r_B = 0.64$), V3CD ($w, p < 0.001, r_B = 0.811$), and V3B ($w, p < 0.001, r_B = 0.922$). Vice versa, the contrast between the LH FEF and the LH IFJ distance-corrected NSC revealed that in the ventral visual stream, several regions had higher connectivity likelihood with the LH IFJ compared to the LH FEF: TGv ($w, p < 0.001, r_B = -0.55$), TE2a ($w, p < 0.001, r_B = -0.603$), TE1m ($w, p < 0.001, r_B = -0.589$) and TE1p ($w, p < 0.001, r_B = -0.732$). The LH FEF had in contrast higher connectivity likelihood with the areas VVC ($w, p = 0.002, r_B = 0.616$), FFC ($w, p = 0.005, r_B = 0.486$) and PIT ($w, p = 0.002, r_B = 0.64$) compared to the LH IFJ. The contrast between the RH FEF and the RH IFJ distance-corrected NSC revealed that in the dorsal visual stream, only one region had higher connectivity likelihood with the RH FEF compared to the RH IFJ, namely 7AL ($w, p = 0.007, r_B = 0.469$), as in our main results. However, we also found that area V3A had a higher connectivity likelihood with the LH IFJ compared to the LH FEF ($w, p = 0.007, r_B = -0.535$) in the distance-corrected outputs. Vice versa, the contrast between the RH FEF and the RH IFJ distance-corrected NSC revealed that in the ventral visual stream, several regions had higher connectivity likelihood with the RH IFJ compared to the RH FEF: TGv ($w, p < 0.001, r_B = -0.906$), TE2a ($w, p < 0.001, r_B = -0.865$), TE1a ($w, p < 0.001, r_B = -0.712$), TF ($w, p < 0.001, r_B = -0.602$), TE1m ($w, p < 0.001, r_B = -0.836$), TE2p ($w, p < 0.001, r_B = -0.729$),

TE1p ($w, p < 0.001, r_B = -0.926$), FFC ($w, p = 0.007, r_B = -0.515$), PH ($w, p < 0.001, r_B = -0.776$), VMV1 ($w, p = 0.006, r_B = -0.848$), and V8 ($w, p = 0.007, r_B = -0.723$).

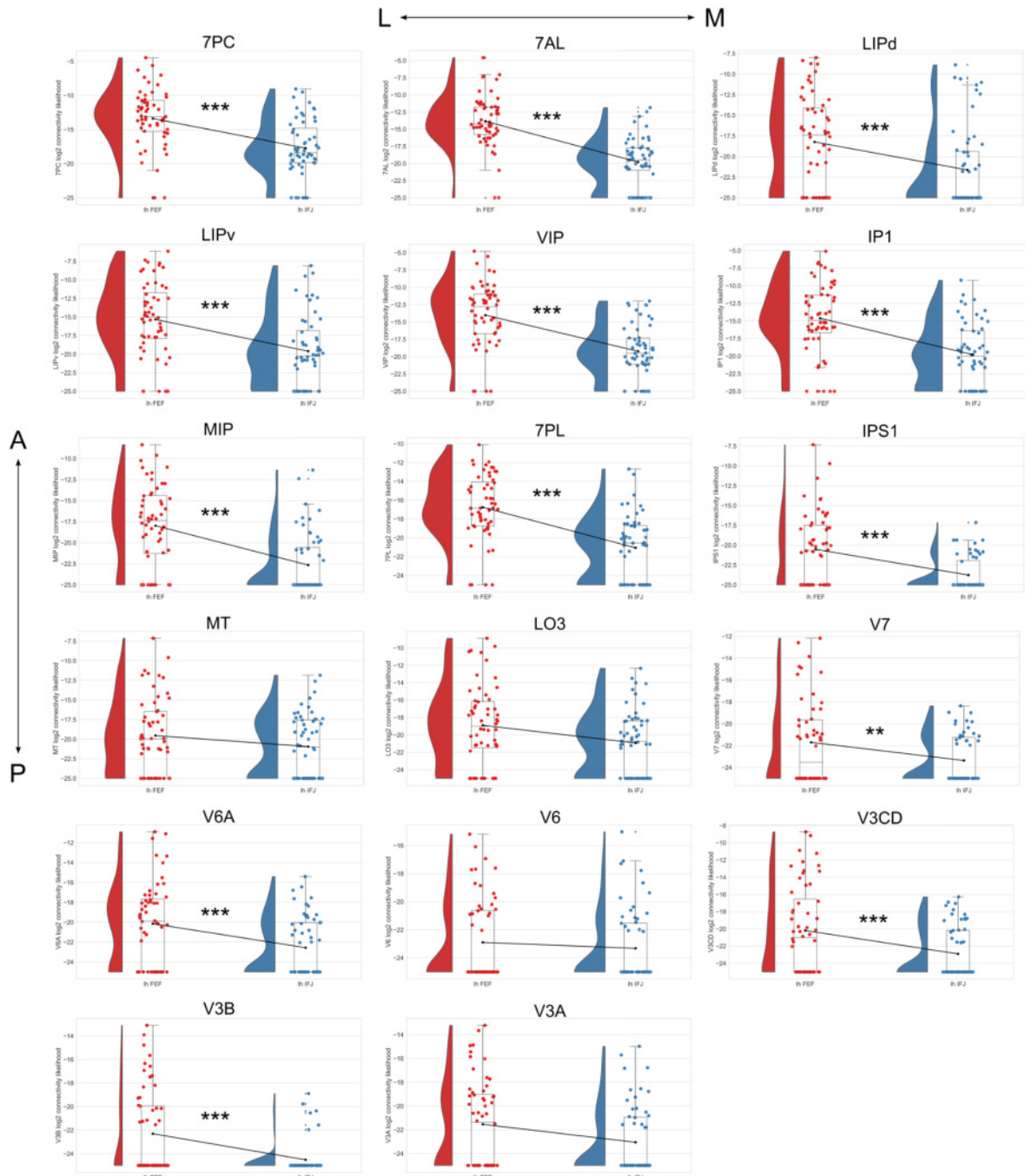


FIGURE 3 Raincloud plots (Allen et al., 2021) of the log-2 scaled NSC of the LH FEF and LH IFJ to each cortical target of the MMP1 from the dorsal visual stream (Glasser et al., 2016; Wang et al., 2015; Zimmerman et al., 2018). A value of -25 is set as an arbitrary log-2 transformed 0 connectivity likelihood for visualization convenience.

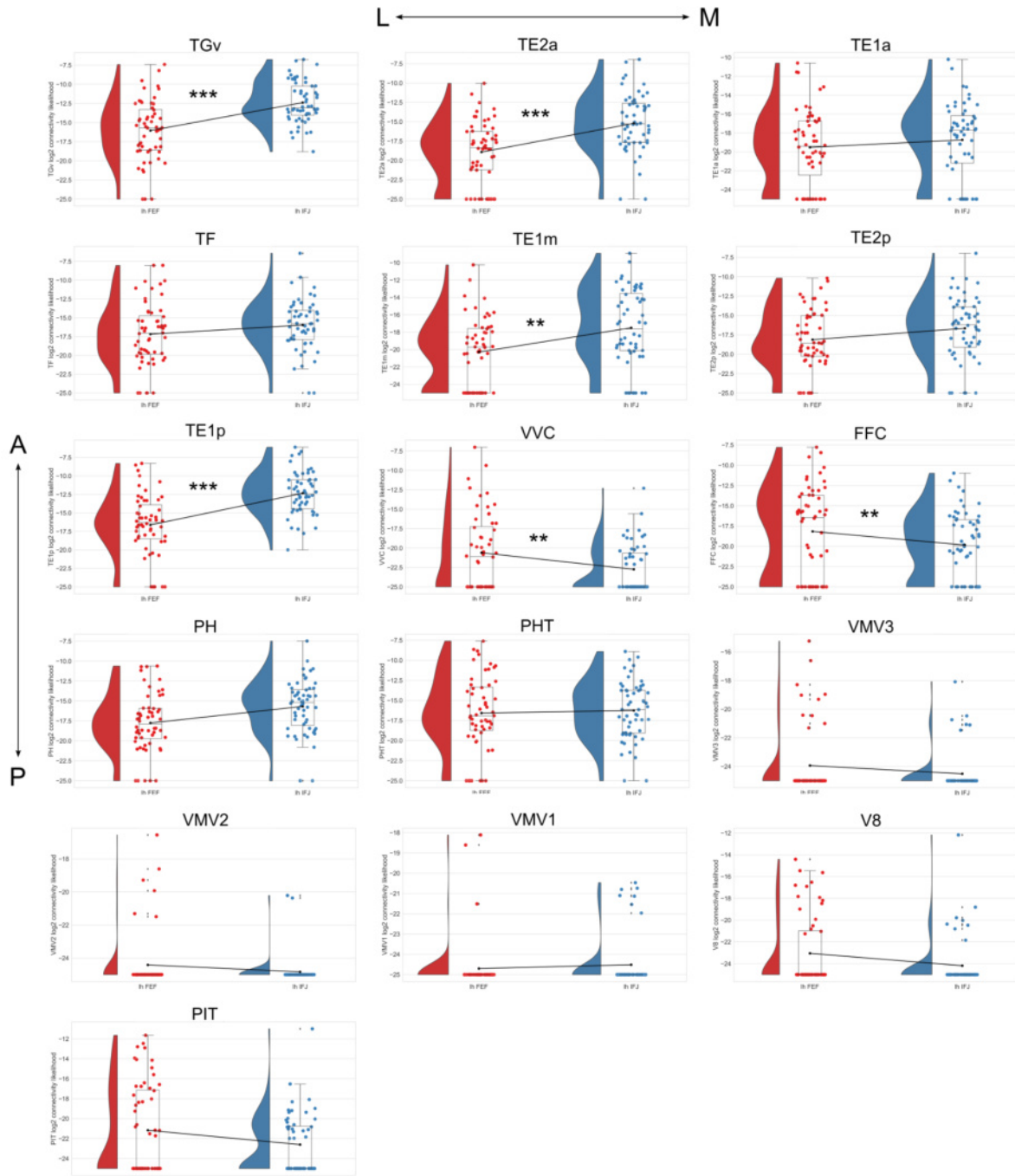


FIGURE 4 Raincloud plots (Allen et al., 2021) of the log-2 scaled NSC of the LH FEF and LH IFJ to each cortical target of the MMP1 from the ventral visual stream (Glasser et al., 2016; Kravitz et al., 2013; Zimmerman et al., 2018). A value of -25 is set as an arbitrary log-2 transformed 0 connectivity likelihood for visualization convenience.

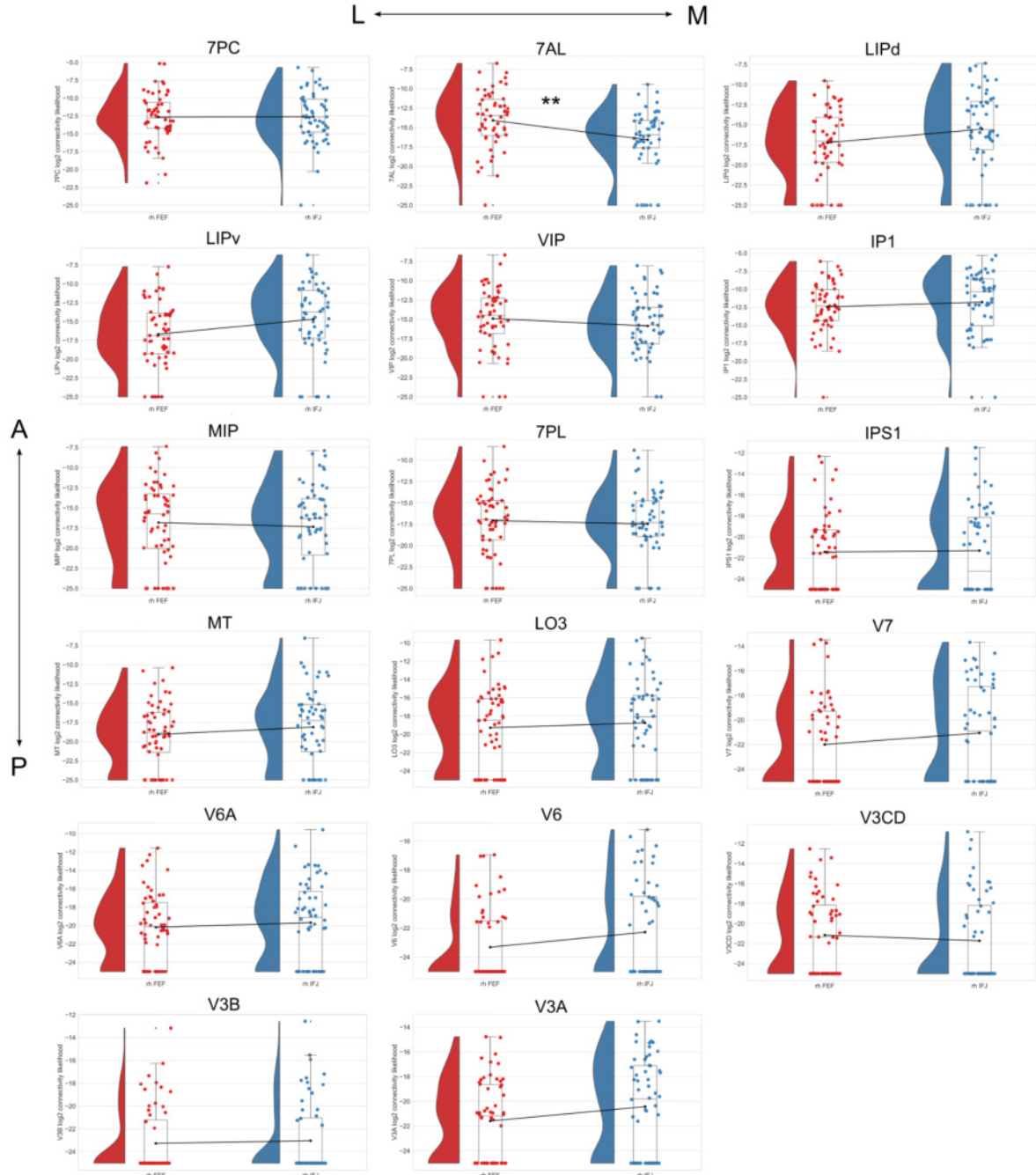


FIGURE 5 Raincloud plots (Allen et al., 2021) of the log-2 scaled NSC of the RH FEF and RH IFJ to each cortical target of the MMP1 from the dorsal visual stream (Glasser et al., 2016; Wang et al., 2015; Zimmerman et al., 2018). A value of -25 is set as an arbitrary log-2 transformed 0 connectivity likelihood for visualization convenience.

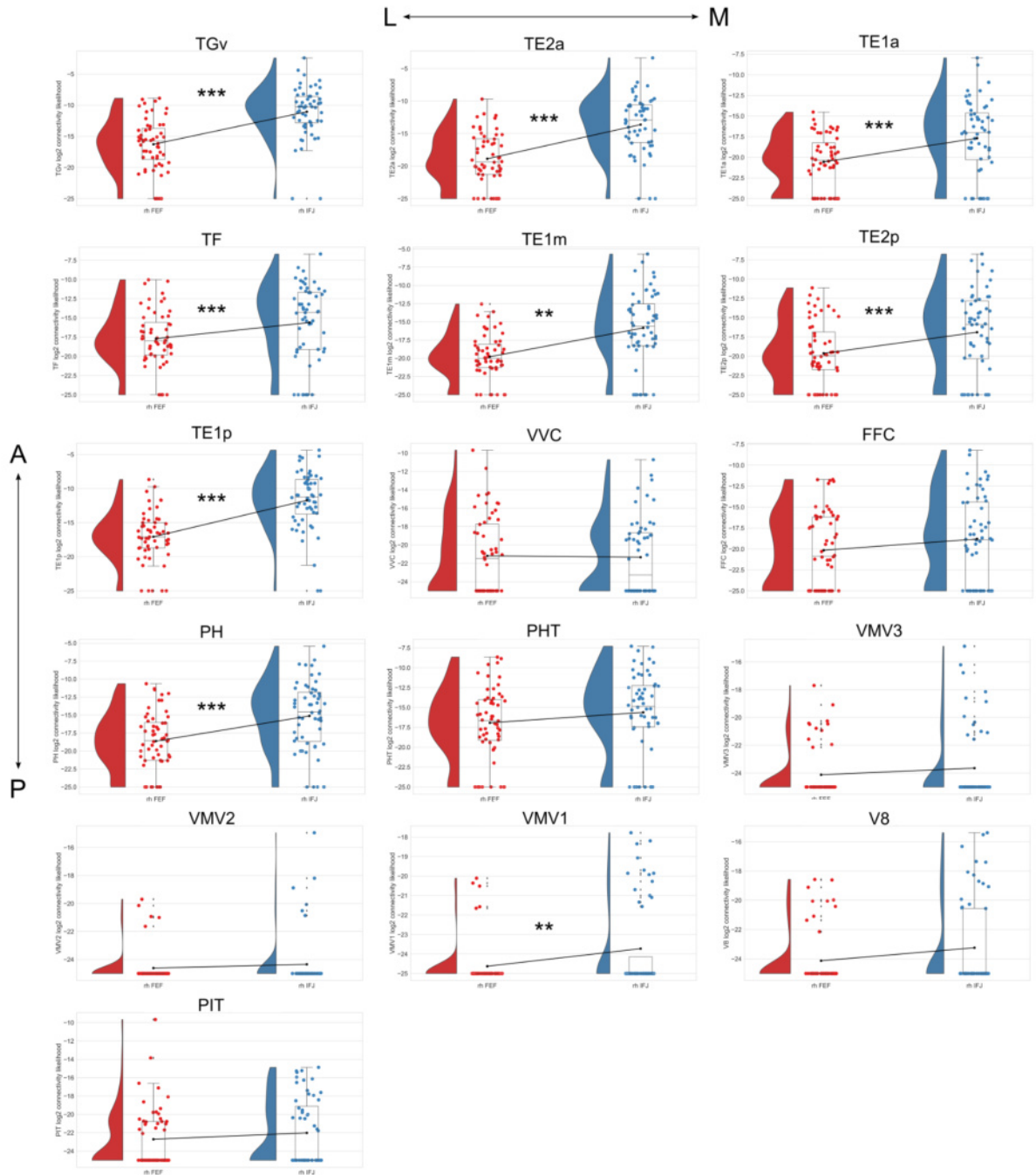


FIGURE 6 Raincloud plots (Allen et al., 2021) of the log-2 scaled NSC of the RH FEF and RH IFJ to each cortical target of the MMP1 from the ventral visual stream (Glasser et al., 2016; Kravitz et al., 2013; Zimmerman et al., 2018). A value of -25 is set as an arbitrary log-2 transformed 0 connectivity likelihood for visualization convenience.

We summarize these results in Figure 7, where the difference in the NSC between LH FEF and LH IFJ, and RH FEF and RH IFJ is visualized on the Conte69 reference space (Van Essen et al., 2012) parcellated using the MMP1 (Figure 7, panel A). All the targets that had a significantly higher connectivity likelihood with either the FEF or IFJ in both the main results and the control analysis for distance are indicated by asterisks in Figure 7, panel B.

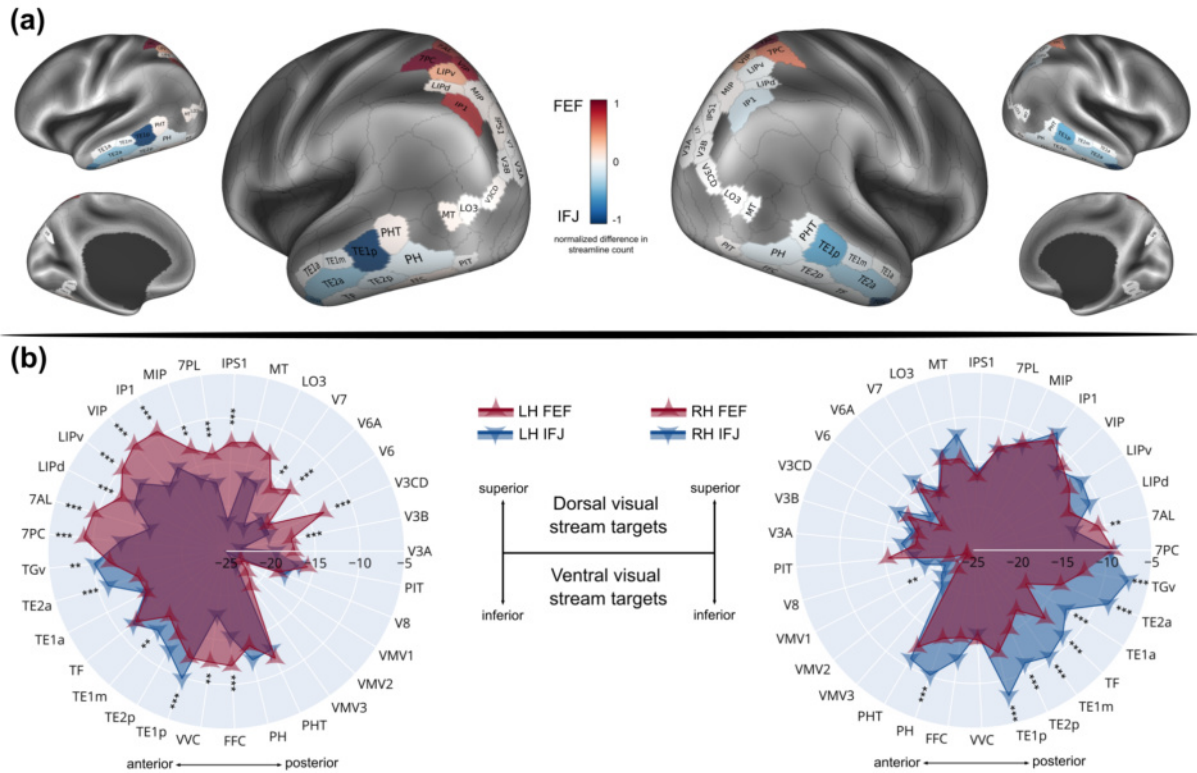


FIGURE 7 **A** Difference in the connectivity likelihood of FEF and IFJ with the dorsal and ventral visual streams visualized on the Conte69 mesh parcellated using the MMP1 schema. Red shades indicate stronger connectivity likelihood with the FEF, and blue shades indicate stronger connectivity likelihood with the IFJ. **B** Spider plots of the log-2 scaled NSC of FEF and IFJ to each cortical target from the MMP1 (−25 is set as a log-2 transformed arbitrary 0 connectivity likelihood for visualization convenience as in the previous figures). Asterisks indicate the significant results in the main analysis and were also replicated and the distance control analysis (** = $p < 0.01$, *** = $p < 0.001$).

4.3.2 Results of the analysis of bundle lateralization and relationship between the FEF and IFJ ALE clusters and the cortical projections of the three branches of the SLF

Our results show that while SLF2 was right-lateralized ($t_{(23)}$, $p = 0.015$, $d = 0.538$), consistent with previous evidence (de Schotten et al., 2011), the SLF3 didn't show evidence of right lateralization. In contrast, the UF was left-lateralized ($t_{(23)}$, $p < 0.001$, $d = -1.198$), and also the AF ($t_{(23)}$, $p = 0.02$, $d = -0.512$), as shown in recent studies (Eichert et al., 2019; Fernández-Miranda et al., 2015). By using our method to estimate the cortical projections of the three branches of the SLF (see Figure 8, panel A), we found differential terminations to

the FEF and IFJ ALE clusters in both hemispheres. In the left hemisphere (Figure 8, panel B), the SLF1 had a significantly higher streamline count that projected to the LH FEF compared to the LH IFJ ($w, p < 0.001, r_B = 0.98$). In contrast, the SLF3 had a significantly higher streamline count that projected to the LH IFJ compared to the LH FEF ($w, p < 0.001, r_B = -0.947$). The analysis of the cortical projections of the SLF2 did not reveal any significant differences. Similarly, in the right hemisphere (Figure 8, panel C), the SLF1 had a significantly higher streamline count that projected to the RH FEF compared to the RH IFJ ($w, p < 0.001, r_B = 0.86$). Again and in contrast, the SLF3 had a significantly higher streamline count that projected to the LH IFJ compared to the LH FEF ($w, p < 0.001, r_B = -0.933$). The comparison of the SLF2 projections didn't reveal any significant differences also in this hemisphere.

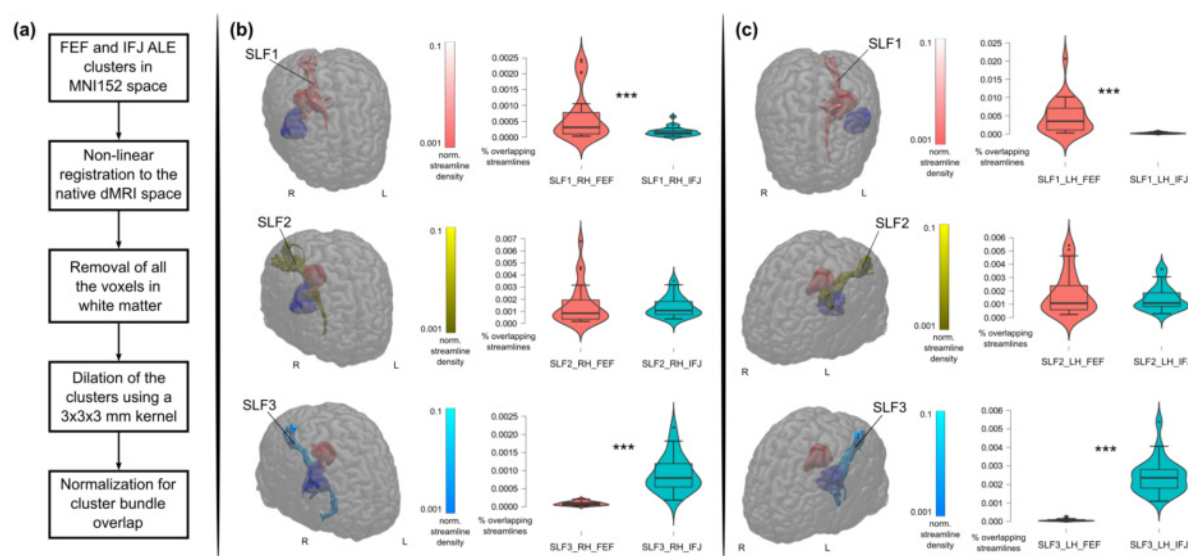


FIGURE 8 **A** Method to estimate the cortical projections of the three branches of the SLF to the FEF and IFJ ALE clusters. **B** Visualization of the segmented SLF1, SLF2, and SLF3 for an example subject overlaid with the dilated FEF and IFJ ALE clusters, and difference in their cortical projections in the right hemisphere. **C** Visualization of the segmented SLF1, SLF2, and SLF3 for an example subject overlaid with the dilated FEF and IFJ ALE clusters, and difference in their cortical projections in the left hemisphere. In both hemispheres, the SLF1 had a higher likelihood of projecting to the FEF ALE cluster, whereas the SLF3 had a higher likelihood of projecting to the IFJ ALE cluster.

4.4 | DISCUSSION

The FEF and the IFJ are prefrontal regions that received increased interest in the field due to their involvement in multiple orchestrating functions (Brass et al., 2005; Vernet et al., 2014). Their overarching role is to provide top-down feedback to bias activity in posterior visual regions in visual attention and working memory tasks (Baldauf & Desimone, 2014; Veniero et al., 2021; Zanto et al., 2011; Zhang et al., 2018). Their structural connectivity patterns are however largely elusive to date. In this study, we combined an ALE

meta-analysis, which allowed us to accurately infer their localization in stereotaxic space, with surface-based probabilistic tractography - to uncover their structural connectivity fingerprints (Passingham et al., 2002) with the dorsal and ventral visual streams (Goodale & Milner, 1992). We parcellated each individual cortex based on the MMP1 (Glasser et al., 2016) to define our target regions, while we used the FEF and IFJ ALE peaks as seeds and propagated streamlines from the WM/GM boundary using powerful anatomically-motivated constraints to our tractography reconstruction. By contrasting the connectivity likelihood of FEF and IFJ in each hemisphere to all the target regions ipsilaterally, we found that in the left hemisphere, the FEF had predominant connectivity likelihood with several regions across the dorsal visual stream, whereas the IFJ had predominant connectivity likelihood with multiple regions of the ventral visual stream. In the right hemisphere, we found predominant connectivity likelihood from FEF to a region in the dorsal stream (i.e., 7AL), and again, predominant connectivity likelihood of the IFJ with several regions of the ventral stream. Overall, we generally found the strongest divergence in these connectivity patterns in regions in the mid to high levels in the visual processing hierarchy of each stream, while it was almost entirely abolished in early visual regions. These patterns underline a gradual rather than absolute transition in the relative area of predominance of FEF and IFJ connectivity, as these regions seemed to be also connected to the targets in the non-dominant stream (particularly the IFJ with parietal regions). Another striking aspect of our results is that they suggest a remarkable hemispheric asymmetry: while in the left hemisphere they largely supported our hypothesis in both streams, in the right hemisphere we found results clearly in line with our prediction only in the ventral visual stream (we offer some suggestions on why this may be the case four paragraphs below). Crucially, we found highly consistent results in our control analysis, where we corrected these connectivity likelihoods based on the average distance traveled by the streamlines to reach their targets from the seeds, thus ruling out this potential confound. Taken together, our findings reveal a reliable anatomical motif of segregated prefrontal pathways connecting the FEF and IFJ to the dorsal and ventral visual streams. These results are consistent with the tract-tracing evidence from the macaque (Gerbella et al., 2010; Schall et al., 1995; Stanton et al., 1993; Webster et al., 1994; Yeterian et al., 2012), and suggest that the two stream architecture may extend into the human PFC, as was first proposed in these comparative studies by Goldman-Rakic and others (Constantinidis & Qi, 2018; Romanski, 2004; Wilson et al., 1993; Yeterian et al., 2012). Using a virtual dissection approach (Catani et al., 2002), we related our findings to the underlying association white matter bundles that form the main frontoparietal and frontotemporal connections (Barbeau et al., 2020; Barrett et al., 2020; de Schotten et al., 2011; Eichert et al., 2019). In terms of the cortical projections to the FEF and IFJ, we showed that the SLF1 streamlines predominantly terminated within the FEF ALE cluster bilaterally, whereas the SLF3 streamlines predominantly terminated within the bilateral IFJ ALE cluster. These two branches of the SLF could underlie the FEF connectivity patterns to the medial and superior parietal cortex, and the IFJ connectivity patterns to the lateral inferior parietal cortex, respectively. The SLF2 instead projected to the FEF and IFJ ALE clusters to the same degree, thus possibly representing a shared pathway mediating their communications with the PPC and its associated functions (Parlatini et al., 2017).

The PFC has typically been conceptualized as the neural substrate of executive functions (Duncan, 2001; Fuster, 2001). Relating activity in specific regions of the PFC to their functional specializations has proven challenging (Assem et al., 2020; Duncan, 2010; Owen et al., 1998; Nee et al., 2013; Wager & Smith, 2003). A promising approach to infer functional specializations relies on comprehensively mapping the connectivity fingerprint of each PFC region (Passingham & Lau, 2022). This hinges on the assumption that the functions of these regions ultimately depend on and are constrained by their unique set of afferent and efferent connections (Mars et al., 2018a; Passingham et al., 2002; Petrides et al., 2012). In our ALE meta-analysis (which used a subset of the results that we extended and discussed in chapter 3), we inferred the localization of FEF and IFJ in standard space based on well-defined functional localizers and tasks that reliably engage these regions. We modeled the uncertainty associated with their localization across several hundreds of subjects (378 for the FEF sample, and 423 for the IFJ sample) and found the highest spatial convergence of activations at the junction of the superior frontal sulcus (SFS) with the sPCS for the FEF, and the junction of the inferior frontal sulcus (IFS) with the iPCS for the IFJ. Using the resulting ALE peaks allowed us to investigate their connectivity in a large dataset by leveraging these coordinates as functionally-derived priors. While previous studies were instrumental in mapping fronto-parietal and fronto-temporal white matter pathways using dMRI tractography (Anderson et al., 2012; Barbeau et al., 2020; Sani et al., 2021; Szczepanski et al., 2013; Umarova et al., 2010), they didn't systematically contrast these connectivity patterns with the lateral PFC. Some initial evidence linking probabilistic tractography to general principles of segregation within the plPFC and premotor regions was reported by Tomassini et al. (2007). The authors showed that the dorsal premotor region had distinct patterns of connectivity with the superior parietal lobule, dorsal PFC and cingulate cortex, whereas in contrast, the ventral premotor region had a higher connection probability with the ventral PFC and anterior inferior parietal lobule. Their connectivity matrices were used to perform a clustering analysis generating a connectivity-based parcellation delineating the boundary between these regions. In a similar vein, Baldauf and Desimone (2014) investigated the connectivity likelihood of the PPA and FFA to structural subdivisions of the PFC, showing that these regions had higher probabilities of being connected with regions localized within the pars triangularis, pars opercularis and the caudal middle frontal gyrus (Baldauf & Desimone, 2014). Another great leap forward in mapping the long-range connectivity patterns that underlie attentional control was the study by Sani et al. (2021). Their comprehensive approach linked fMRI activity with the comparative mapping of the reciprocal connections between FEF, LIPd and a newly proposed attentional control node in the posterior temporal cortex (i.e., phPIT). Area phPIT showed a general absence of significant modulation across the various fMRI tasks employed to localize it (but only by the locus of attention), thus suggesting that no feature tuning is present in this area, and leading the authors to suggest that it may represent a priority map (Fecteau & Munoz, 2006; Zelinsky & Bisley, 2015). Despite this, their interpretation needs to be supported by further evidence that is not based solely on univariate analyses, but also on methods capable of fully capturing its activation profile, such as MVPA. The possibility of some form of functional specialization in these nodes (FEF, LIPd, phPIT, and IFJ) raises the question of whether the connectivity patterns in

the control nodes of the attention and frontoparietal network could be organized according to the representational content encoded, rather than possessing a domain-general organization (Liu & Hou, 2013), as I suggested in chapter 1 of this dissertation. Our study ties into these efforts by providing tractography evidence that the PFC, and more precisely the FEF and IFJ, two crucial attentional control structures, communicate through segregated anatomical pathways to the dorsal and ventral streams. Our results suggest that their connectivity fingerprints may enable these regions to efficiently bias activity in the mid to high-level regions in the respective visual processing hierarchy. By characterizing their distinctive patterns of anatomical connectivity, our study highlights potential white matter pathways associated with the types of attentional control (spatial vs non-spatial), and opens the possibility to fractionate prefrontal networks based on their stimulus domain (Liu & Hou, 2013; Markett et al., 2021; Parlatini et al., 2017; Rajan et al., 2021).

Our probabilistic tractography methodology was carefully modeled on the approach reported in Donahue et al. (2016), a study in which the authors were able to validate their results based on retrograde tracer injections. Using the high quality and resolution provided by the 3T HCP dMRI data (1.25mm isotropic), and performing all our analyses in the native subject space, we strived to preserve the detailed anatomy of each individual brain. We parcellated the cortex according to the MMP1 schema, one of the most comprehensive brain atlases available to date. By mapping the MMP1 to each individual white matter surface using FreeSurfer registration (Fischl et al., 1999), we fully exploited its high resolution that is often deteriorated in studies performing analyses in volumetric space (Coalson et al., 2018). We non-linearly registered the FEF and IFJ ALE peaks to each subject native space and projected the resulting spheres on the white matter segmentation as well. Our probabilistic tractography approach was designed to include as many anatomical constraints based on our specific hypothesis to optimize the reconstruction of long-range cortico-cortical connections (Jbabdi et al., 2015). In particular, by seeding from the WM/GM boundary and using the pial surface as a termination mask we attempted to mitigate some of the biases affecting tractography (Schilling et al., 2017; Van Essen et al., 2013). Firstly, the use of a pial termination mask allows to discard streamlines that would incorrectly propagate between adjacent gyri (Hernandez-Fernandez et al., 2019). Secondly, we chose the WM/GM seeding approach as several studies show that it is beneficial in alleviating the gyral bias affecting tractography reconstruction (Schilling et al., 2017), as well as in reducing partial volume effects (Cottaar et al., 2021; Kleinnijenhuis et al., 2015; Parvathaneni et al., 2019; Roine et al., 2014; Smith et al., 2012) and length biases (Girard et al., 2014). Having the MMP1 projected on the white matter surface improves the assignment of the streamline terminations to the nearest cortical label (St-Onge et al., 2022; Yeh et al., 2019). Finally, several ‘avoid’ masks, which included the segmentations of subcortical nuclei, the corpus callosum, and the cerebellum, were added to further discard invalid streamlines that would potentially result in tracking false positive connections (Hernandez-Fernandez et al., 2019).

In recent years, several attempts have been made to validate tractography results, including the use of phantoms, *ex-vivo* data and tracer injections (Jbabdi et al., 2013a; Grisot et al., 2021; Maier-Hein et al., 2017; Sarwar et al., 2022). These initiatives, which have also

taken the form of challenges to reconstruct well-known white matter bundles using different algorithms (Maier-Hein et al., 2017), provided critical information on tractography limitations and typical pitfalls (Calamante, 2019; Grisot et al., 2021; Reveley et al., 2015). In this sense, even though we relied on the most up to date FSL pipeline (Hernandez-Fernandez et al., 2019) and processing practices for tractography that were validated on tracer injections as a ‘silver standard’ (Donahue et al., 2016; Sarwar et al., 2021), it must be noted that some of these limitations are also likely to affect our results. Perhaps the most important of these is the tendency of tractography algorithms, including FSL’s probtrackx, to generate a considerable number of false positives (Donahue et al., 2016; Maier-Hein et al., 2017). Our strategy to limit these was based on a priori anatomical information, which we transferred in our tractography analysis by using termination and avoid masks, tracking only ipsilaterally and to a limited number of targets ($n = 33$). Our statistical comparisons between FEF and IFJ NSC were restricted to these targets, and we applied FDR to further reduce the number of false positive findings about the divergence in these connectivity likelihoods. However, it is likely that densely sampling the fiber orientations inferred with bedpostx using 50000 streamlines per vertex to increase our sensitivity may have led to inadvertently increasing the number of non-plausible streamlines. We would therefore like to acknowledge that a computational strategy to filter out these streamlines would be beneficial (Daducci et al., 2014; Pestilli et al., 2014; Smith et al., 2015). Currently, FSL doesn’t include a post-processing step to filter out spurious streamlines, although the information about the uncertainty in the connectome reconstruction is already built-in the analysis pipeline (Jbabdi & Johansen-Berg, 2011). More specifically, probtrackx’s outputs index the probability that a region is on the dominant pathway of anatomical connectivity from a seed region (Jeurissen et al., 2019). Hence, regions with low streamline counts should be the pathways that are less reproducible and contain a greater amount of false positives. However, this measure is in turn influenced by various factors which are often difficult to control, such as the distance, the size of the target regions, and finally the noise in the data (Jbabdi & Johansen-Berg, 2011). When we applied a distance correction based on the average length of the streamlines to our NSC, as done in previous studies (Hagmann et al., 2008; Roberts et al., 2016), we were able to replicate our main results, with minor exceptions where the previous effect was no longer significant. Some of our comparisons seemed however inconclusive, especially in lower visual regions. For example, for areas V3B and V6 in the dorsal stream, and areas V8, VMV1, VMV2, and VMV3 in the ventral streams, we did not find an NSC higher than 0 in more than half of our subjects for both the FEF and IFJ seeds. Thus, using this as a heuristic criterion, we can consider these comparisons not well supported by the evidence. It is possible that by propagating streamlines from the full spatial extent of the FEF and IFJ region, some of these target regions would show reliable connectivity with these seeds. Our goal was to however keep the seeds as spatially focused as possible in order to maximize the probability of tapping into the subject-specific FEF and IFJ, as our definitions were based on a meta-analysis and not direct data from an fMRI localizer task performed by each subject. The visual inspection of our projection step (Figure 2, panels B and C) confirms that our seeds were in most cases correctly placed at the junction of the SFS and sPCS (for FEF), and the junction of the IFS and iPCS (for the IFJ), which gives us strong anatomical clues that

these should be localized within the individual functional regions of interest. Another critical aspect of our seeding strategy is the fact that we only tracked from these regions, and not symmetrically, from seeds to targets and vice versa (as done for example in Rosen & Halgren, 2021). As the FEF and IFJ seeds were however often placed either on the walls or the fundus of one of the adjacent sulci, tracking from the dorsal and ventral stream target regions to the seeds would possibly have resulted in severe artifacts and increased inter-individual variability due to the gyral bias (Schilling et al., 2017; Van Essen et al., 2013). It seems reasonable to hypothesize that the connections between our seeds and targets that we reported here are largely reciprocal, and thus include both afferent and efferent connections (Jbabdi & Johansen-Berg, 2011), although our method doesn't allow us to distinguish between these possibilities.

To uncover the association white matter bundles underlying the connectivity between FEF and IFJ and the posterior visual streams, we carried out the virtual dissection of the AF, SLF1, SLF2, SLF3, and UF (Barrett et al., 2020) using the protocols described in Warrington et al. (2020) in a subsample of 24 subjects. We developed a method to project the streamlines of the SLF1, SLF2, and SLF3 and to estimate their cortical terminations relative to the FEF and IFJ ALE clusters, which were registered to the native dMRI space of each subject. By contrasting the normalized count of these projected streamlines, we showed that the SLF1 predominantly projected to the FEF ALE cluster in both hemispheres, while the SLF3 predominantly projected to the IFJ ALE cluster in both hemispheres across subjects. These results are well in line with those reported by de Schotten et al. (2011), who first highlighted the relationship between the three branches of the SLF and the DAN and VAN (Corbetta & Shulman, 2002). With respect to our surface-based tractography, these results suggest that the main pathway of communication between the FEF and the SPL may be the SLF1, and the one between the IFJ and the inferior parietal lobule and angular gyrus (including some regions that were however not part of our hypothesis) may be the SLF3. The analysis of the projections of the SLF2 suggested that this branch may be a shared pathway from these seeds to the PPC (Parlatini et al., 2017). Interestingly, as reported in de Schotten et al. (2011), the SLF2 was right-lateralized (Bartolomeo & Seidel Malkinson, 2019). This may in our opinion provide a way to reconcile the hemispheric differences in our tractography results for the dorsal visual stream. In fact, while for the LH FEF we found strong divergence in its connectivity likelihoods with this stream compared to the LH IFJ, in the right hemisphere we did not find significant differences, with the exception of a single target region (7AL; see Figure 7), which is localized in the dorsal and anterior SPL. Quantitatively, it seems that these results are driven by an increased connectivity likelihood of the RH IFJ with this stream, as opposed to a decrease in the connectivity likelihood of the RH FEF per se (see Figure 7, panel B). If we take into account the larger volume of the RH SLF2 and the fact that its terminations are localized in the PPC, this may provide a basis for these discrepancies in the divergence between the FEF and IFJ fingerprints in the two hemispheres, although this interpretation would need to be examined in a separate study. Consistent with this idea however, a recent study examining the structural connectivity of the DAN and VAN showed that both networks are right-lateralized (Alves et al. 2022). I suggest that the connections between the IFJ and parietal regions could support its increased involvement in the DAN in

the right hemisphere. Regarding the connections of the IFJ with the ventral visual stream, we hypothesize that they could be mediated by the AF and the UF based on our virtual dissection results. Classically, the AF connects the ventro-lateral PFC to areas of the middle temporal lobe (Fernández-Miranda et al., 2015; Rilling et al., 2008). Recent studies have refined our understanding of the organization of this bundle (Eichert et al., 2019), providing more accurate indications on its connectional anatomy. The UF runs from the ventro-lateral PFC, and reaches the anterior temporal lobe. This bundle was already implicated in the connectivity of the IFJ using deterministic tractography (Baldauf & Desimone, 2014). This bundle's anatomy is however difficult to examine in detail using virtual dissection approaches as its fibers form a continuum that runs through the extreme capsule along with the extreme capsule fascicle and the IFOF (Weiller et al., 2021). Although the AF and UF showed evidence of left lateralization, these asymmetries didn't seem to drive our results, as the LH and RH IFJ connectivity patterns with the ventral visual stream were largely similar.

In summary, using surface-based probabilistic tractography in this study we present evidence that the FEF has a predominant connectivity likelihood with regions of the dorsal visual stream compared to the IFJ (particularly in the left hemisphere), whereas in contrast, the IFJ has a predominant connectivity likelihood with regions of the ventral visual stream. These patterns are mediated by long-range association bundles, including the SLF1, SLF2, SLF3 (D'Andrea et al., 2019; Marshall et al., 2015a), and the AF and UF. These findings highlight a general anatomical motif of reciprocal segregated white matter pathways from the PFC and the dorsal and ventral visual streams, suggesting that the two visual stream architecture may extend into the PFC, as was first proposed based on comparative evidence (Romanski, 2004; Wilson et al., 1993; Yeterian et al., 2012). These findings further support the idea of the functional specialization of the FEF and IFJ for spatial vs non-spatial processing in attention and working memory functions. Based on its set of input and output connections, the FEF seems to be optimally placed within the visual processing hierarchy (Felleman & Van Essen, 1991) to efficiently bias spatial selection and spatial working memory in posterior visual regions (Marshall et al., 2015b; Ruff et al., 2006; Veniero et al., 2021). Similarly, the IFJ receives afferent connections and sends feedback to regions across the ventral stream to efficiently bias non-spatial (feature- and object-based) selection and working memory (Baldauf & Desimone, 2014; Zanto et al., 2011; Zhang et al., 2018). These connectivity patterns suggest a simple yet important principle in how the attention networks may be organized, that is, in a domain-specific manner. In the spatial domain, it is well established that spatial maps are encoded by each region at the neural population level (Dumoulin & Wandell, 2007; Sprague & Serences, 2013). These topographic maps are present throughout the visual hierarchy, culminating in the PFC where they overlap with the FEF (Kastner et al., 2007; Mackey et al., 2017). Adjacent topographic representations of the visual field have been shown to be structurally and functionally wired across several regions in the visual and parietal cortex (Greenberg et al., 2012; Heinzle et al., 2011; Mohavedian Attar et al., 2020). Recently, preferential connectivity between the far-peripheral and the central visual field representation has been uncovered in frontal regions and V1 combining a dMRI and resting-state fMRI structural and functional connectivity analysis using HCP data

(Sims et al., 2021). These patterns of preferential connectivity between topographically similar representations of the visual field may provide a computationally efficient mechanism for top-down spatial selection (Jbabdi et al., 2013b). In the case of non-spatial mechanisms, it is arguably much more difficult to pinpoint a structure of this kind. Comparative studies have however begun to elucidate the organization of the ventro-lateral PFC in the form of selective cortical patches (e.g., face patches; Haile et al., 2019; Tsao et al., 2008). We suggest that in principle this form of organization could provide a similar substrate of preferential connectivity across different stimuli in feature and object space (Chang et al., 2017; Haile et al., 2019; Lafer-Souza et al., 2016). In conclusion, in this study, we uncovered the patterns of structural connectivity of the FEF and the IFJ with the dorsal and ventral visual streams. These regions have been implicated in several functions including attention, working memory and cognitive control. By combining an ALE fMRI meta-analysis with surface-based tractography, we revealed that these orchestrating functions may be ultimately grounded in their structural connectivity fingerprints (Osher et al., 2016; Passingham et al., 2002).

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Chapter 5

General Discussion

In this dissertation, I aimed at characterizing the connectivity fingerprints of the Frontal Eye Field (FEF) and the Inferior Frontal Junction (IFJ) to uncover how they may contribute to their specialized roles within the prefrontal cortex (PFC). In particular, my main goal was to investigate dissociations between these two regions based on the general idea of a dorso-ventral gradient organization in the posterior-lateral PFC, according to which dorsal regions would be specialized for spatial processing, and ventral regions would be specialized for non-spatial processing. Therefore, I tried to infer the most consistent localization of these regions in standard space via a coordinate-based meta-analysis, and by using this information, to map their coactivation patterns and structural connectivity fingerprints with the posterior dorsal and ventral visual streams. I will review the main findings presented in the previous chapters below, discuss their theoretical implications for understanding the function of the PFC and its associated networks, and present some potentially interesting avenues for future research.

5.1 | SUMMARY OF THE FINDINGS

I started by carrying out a comprehensive review of the literature on the structure, function and connectivity of the FEF and the IFJ, two crucial control structures localized in the posterior-lateral PFC (chapter 2). This review was primarily focused on neuroimaging studies in humans but also drew heavily from decades of prior comparative research in non-human primates, which provided a clear theoretical framework for understanding the functional organization of the PFC (Chafee & Heilbronner, 2022; Fuster, 2001; Goldman-Rakic, 1996; Martinez-Trujillo, 2022). Briefly, my review highlighted several key similarities and differences between the FEF and IFJ: 1. Both regions are characterized by a dysgranular architecture (i.e., by a weakly developed layer IV); 2. The localization of both regions is tightly linked to specific anatomical landmarks, namely the junction of the superior frontal sulcus (SFS) and the superior precentral sulcus (sPCS) for the FEF, and the junction of the inferior frontal sulcus (IFS) and the inferior precentral sulcus (iPCS) for the IFJ; 3. Their activity is driven by visual stimulation, but only the FEF seems to be topographically organized, as shown by fMRI retinotopic mapping studies; 4. Both regions are involved in top-down attention, but the IFJ is also involved in tasks where there are strong bottom-up components; 5. A dissociation in the functions of the FEF and IFJ based on the relative predominance in mediating spatial vs non-spatial (feature- and object-based) attention and working memory, and finally; 6. The inclusion of the IFJ in the core of the multiple demand system. This review allowed me to identify some of the most important open questions regarding the role of these regions, among which I pursued what in my opinion were the most urgent ones, which are at the core of this dissertation. While as introduced in point 2, the FEF and IFJ seemed to be tied to specific anatomical landmarks, in that chapter a preliminary analysis of the coordinates reported across different studies and meta-analyses revealed the presence of a substantial variability, particularly along the sagittal plane. This further motivated the need to perform a systematic reanalysis of the fMRI literature to accurately infer the localization of these regions in stereotaxic space. This research goal was attained in chapter 3 via a coordinate-based meta-analysis by using the activation likelihood estimation (ALE) technique, which allows modeling the convergence of the activations reported across

studies (and groups of individuals). For this analysis, I included only well-validated localizer paradigms and tasks that reliably engage these regions. Prosaccade and antisaccade paradigms were included in the FEF meta-analysis sample, and oddball/attention, working memory, task-switching and Stroop paradigms were included in the IFJ meta-analysis sample. This enabled me to further substantiate the relationship of the FEF and the IFJ with the sulcal landmarks described previously (SFS, sPCS, IFS, iPCS) and derive their localization using their ALE peaks as a proxy within the respective clusters of activation. Although our results were generally consistent with previous evidence, we also highlighted some discrepancies with previous meta-analyses, both in terms of their methodology and results and the taxonomy of regions proposed in the multimodal parcellation (MMP1) by Glasser et al. (2016). Next, by using these ALE coordinates as seeds I performed a meta-analytic connectivity modeling analysis to uncover their whole-brain coactivation patterns in a fully data-driven fashion. The results revealed the broad and systematic coactivation patterns of the FEF and IFJ with other frontal, parietal and temporal regions, and allowed me to decode the behavioral domains associated with them via a reverse inference. In chapter 4, I leveraged the unprecedented data quality of the Human Connectome Project to carry out the analysis of the structural connectivity of the FEF and IFJ using the 3T diffusion MRI data (Sotiropoulos et al., 2013) from 56 healthy subjects. I combined a surface-based probabilistic tractography analysis with the virtual dissection of the white matter bundles connecting the FEF and IFJ to the posterior parietal and temporal cortices. Contrasting the connectivity likelihood of the FEF and IFJ with the dorsal and ventral visual streams parcellated using the MMP1 revealed a higher connectivity likelihood of the FEF with dorsal stream regions compared with the IFJ (which was best supported in the left hemisphere), and vice versa a higher connectivity likelihood of the IFJ with ventral stream regions compared with the FEF. These results were complemented by the analysis of the cortical terminations of the superior longitudinal fasciculus (SLF), which implicated two of its branches (the SLF1 and SLF3) in providing segregated routes of communication between the FEF and IFJ to the superior and inferior parietal lobule, respectively.

5.2 | IMPLICATIONS FOR UNDERSTANDING THE ORGANIZATION OF THE PREFRONTAL CORTEX

The structure of executive control in the PFC has often been conceptualized as an entangled unit given that some regions can respond to different manipulations at the same time, while flexibly varying their responses to each based on the experimental context (Duncan, 2010; Miller & Cohen, 2001). The emergence of multivariate techniques to analyze neuroimaging data (MVPA; Haynes & Rees, 2005; Kamitani & Tong, 2005), and the contributions of non-invasive approaches to investigate brain connectivity (Jbabdi et al., 2015; Sporns et al., 2005) have however allowed researchers to increasingly probe this structure and uncover specializations within the PFC over the past two decades. Taken together, the results I presented in this dissertation support the idea that the functional specialization of the FEF and IFJ critically depends on their connectivity patterns (Osher et al., 2016; Passingham et al., 2002; Saygin et al., 2012). In particular, my results suggest that similar to the macaque (Costantinidis & Qi, 2018; Wilson et al., 1993), the two visual stream

architecture extends into the human PFC, and they highlight a dorso-ventral gradient organization in the posterior-lateral PFC (O'Reilly, 2010). These results fit well with ongoing trends in the fMRI literature which pursue the careful mapping of prefrontal networks at the individual subject level. The study by Michalka et al. (2015) identified visually and auditory biased regions in the posterior-lateral PFC using attention and change detection tasks followed by their resting-state fMRI analysis. Recently, Lefco et al. (2020) capitalized on a similar approach and used resting-state fMRI to investigate the detailed intrinsic connectivity patterns of the frontoparietal network (FPN), which included the dorsal attention network (DAN; Corbetta & Shulman, 2002) and the cognitive control network (CCN; Cole & Schneider, 2007). The authors defined three prefrontal ROIs corresponding to the sPCS, the iPCS and the mid-IFS using the contrast between 2-back visual vs auditory working memory blocks. They then investigated the fine-grained connectivity patterns of these regions with retinotopic regions in the posterior parietal cortex (PPC) and computed difference maps between each ROI and the remaining ROI pairs. Importantly, the intrinsic connectivity patterns of the iPCS and sPCS regions (which seem to correspond well to the IFJ and FEF) were increased with PPC regions that represented the central vs the peripheral visual field, respectively. In the PPC, these formed an ordered dorso-medial to ventro-lateral gradient. Overall, these and previous other studies (Mackey et al., 2017; Noyce et al., 2017; Tobyne et al., 2017) strongly suggest the presence of robust sensory biases in the PFC, which in turn depend on the underlying connectivity patterns with posterior cortices that constrain the information that each region receives and sends in the form of feedback signals (Passingham & Lau, 2022). In this context, I shall emphasize that the hypothesis of specialized and multiple demand regions in the PFC need not be mutually exclusive. In line with this idea, using improved data alignment between subjects and surface-based methods, Assem et al. (2021) found that multiple demand regions lie side by side with these sensory-biased specialized modules (Tobyne et al., 2017). The authors hypothesize that these modules are positioned to feed modality-specific information to adjacent multiple demand regions, thus being critical to enabling their integrative function (Assem et al., 2021). The results presented in this dissertation similarly leverage surface-based methods for atlas registration and tractography analysis, and contribute to highlighting the FEF and IFJ as specialized components of this complex mosaic organization.

5.3 | THE ROLE OF THE WHITE MATTER IN LARGE-SCALE BRAIN NETWORKS

Our current understanding of the organization of the brain in large-scale networks mostly derives from fMRI (Ji et al., 2019; Yeo et al., 2011). The activations measured in different tasks with fMRI are often recapitulated in stable resting-state fMRI patterns (Fox et al., 2006; Vincent et al., 2008), which are captured by computing correlations between voxels or regions, and clustering and other techniques may be then applied to delineate segregated whole-brain networks (Yeo et al., 2011). Of interest here, albeit with some notable differences in the specific terminology adopted by different research groups (Uddin et al., 2019), the FEF and IFJ have been often implicated in distinct networks. The FEF has been implicated in the DAN (Corbetta & Shulman, 2002; Fox et al., 2006) or cingulo-opercular network more

recently (Ji et al., 2019). The IFJ has instead been implicated in the CCN (Cole & Schneider, 2007), the FPN and language networks (Ji et al., 2019), or more rarely the DAN. While these network taxonomies may be clearly useful for understanding broad interactions between regions at the systems level, they seem to oversimplify the role of prefrontal regions, which may participate in several networks depending on the experimental context. This was exemplified in the results I presented in chapter 3 (see the meta-analytic connectivity modeling results), where the coactivations of the FEF and IFJ resembled specific resting-state networks in terms of their topographies (the DAN for the FEF, and the CCN for the IFJ), but revealed reliable associations with far more behavioral domains than what would be assumed based on these simplified taxonomies. At the same time, it should be noted that canonical resting-state networks may not be necessarily grounded in the structural connectivity patterns between their nodes, as the correlations between their activity may be driven by direct and/or indirect (i.e., monosynaptic or polysynaptic) connections (Jbabdi et al., 2015). Although these aspects (structural and functional connectivity) often go hand in hand (Vincent et al., 2007), studies in humans have often presupposed this link without explicitly comparing the two. With regards to the attention networks for example (i.e., DAN and VAN; Corbetta & Shulman, 2002), examining the white matter architecture seems to provide a more accurate and complete picture of their organization. I discussed the study by Sani et al. (2021) in chapter 4, which reported evidence of posterior-temporal node (phPIT) interconnected with FEF and LIP that encodes attentional priority, as shown by the fact that it wasn't tuned for any particular visual feature. That study seems to suggest that the attentional control architecture may be even more distributed than what is currently thought (Fiebelkorn & Kastner, 2020), and tractography played a decisive role in that discovery. A similar structural/functional approach was adopted in the study by Alves et al. (2022), where the authors investigated the subcortical architecture of the DAN and VAN. By combining the analysis of resting-state fMRI data of seed regions derived from an fMRI parcellation (Gordon et al., 2016), with the analysis of their structural connectivity using dMRI, the authors were able to elucidate the organization of the DAN and VAN in subcortical nuclei, and the structural connectivity between their cortical and subcortical nodes. The structural connectivity between DAN cortical nodes was mediated by the SLF1, whereas vice versa the SLF3 mediated the connectivity between the VAN nodes. These results are consistent with those reported in chapter 4 in the virtual dissection approach, which established a link between the cortical projections of the SLF1 to the FEF and of the SLF3 to the IFJ. Moving past the top-down vs bottom-up attention dichotomy that is associated with the DAN and VAN resting-state parcellation however, the results presented in this dissertation raise the question of whether the attention networks may be also organized according to the visual stimuli domains (spatial, non-spatial) rather than having a domain-general and feature-agnostic organization. Such a hypothesis could pave the way to further fractionate these networks (Liu & Hou, 2013; Markett et al., 2021; Rajan et al., 2021) and may in turn impact our current understanding of the mechanisms of visual attention and working memory. From a strictly biophysical perspective, large and strongly myelinated white matter bundles should allow reliable transmission (i.e., with fixed conduction times) of signals from prefrontal to posterior regions and vice versa (de Schotten & Forkel, 2022), thus providing a

structural scaffold for electrical signals to propagate by means of coherent neural oscillations (Fries, 2015). These signals may be important to bias visual processing online (in visual selection; Baldauf & Desimone, 2014), or offline, by sustaining sensory representations in posterior visual cortices (in working memory; Serences, 2016). Effects of such kind have started to be elucidated in detail in the macaque brain, where functional connectivity, coherence and Granger causality in different frequency bands have been related to the connectivity between regions as their anatomical backbone (Vezoli et al., 2021). The present dissertation doesn't provide such evidence in humans, and the goal of future studies should be to address these correlations between structural and functional connectivity by simultaneous analysis of multiple modalities (dMRI, fMRI, MEG) and non-invasive stimulation approaches (TMS-fMRI, TMS-EEG). I will try to outline other interesting future directions in the last section of this dissertation.

5.4 | FUTURE DIRECTIONS

As I have underlined throughout my dissertation, the concept of connectivity fingerprints is of paramount importance to understanding functional specialization within the PFC (Passingham & Lau, 2022). While the results presented in chapters 3 and 4 offer critical evidence in this direction, they don't explicitly accomplish such a link experimentally. I suggest that ultimately, a powerful benchmark to evaluate the hypothesis that the functions of FEF and IFJ are constrained by their connectivity fingerprints is afforded by the possibility of using these to predict their localization in new subjects (Cole et al., 2016; Osher et al., 2016; Saygin et al., 2012; Tavor et al., 2016). More specifically, these connectivity fingerprints may be inferred using dMRI, fMRI and source-reconstructed MEG data, and used to identify groups of voxels/vertices that show similar profiles using a cross-validation approach. Finally, running fMRI localizer tasks, such as the ones described in chapter 3, should provide an unbiased way of comparing the predicted vs actual localization of these regions. This approach has already been successfully implemented by Osher and colleagues (2019) to predict activity within the DAN by using each subject's whole-brain resting-state fMRI patterns. A change detection task was used to inclusively mask all the regions from the MMP1 that were activated across every subject to form their DAN search space. Then, the authors computed the functional connectivity of each node with all the other regions of the MMP1 (the target space) and used these patterns to predict activity in a leave-one-subject-out approach. They showed that the model predicting activity using each subject's own functional fingerprint outperforms in accuracy a group-level and other subjects' connectivity models. Interestingly, the most informative prefrontal nodes in this study included the FEF and IFJ, which were shown to be strong predictors of activity in the parietal cortex. Conversely, it was also shown that retinotopic regions from the dorsal visual stream and posterior temporal regions from the ventral visual stream were the strongest predictors of prefrontal activations, which supports the idea that regions that are coactive during the task (even outside the DAN) are also the most predictive of activity within the DAN (Osher et al., 2019). These results open up the possibility of investigating the structural connectivity between these sets of regions to see whether they lead to similar predictive power in localizing DAN activations, as

shown in previous studies in extrastriate visual regions (Osher et al., 2016; Saygin et al., 2012).

A fundamental inspiration for this dissertation came from the studies that, thanks to tracer injections, carefully mapped the connections between the macaque PFC and posterior regions (Yeterian et al., 2012). In parallel to this, neurophysiological studies were also instrumental in refining the model of PFC function in the macaque (Martinez-Trujillo, 2022). Bichot et al. (2015, 2019) systematically inactivated the ventral pre-arcuate region (VPA) and assessed the effects on behavior in a visual search task. VPA inactivation abolished the behavioral advantages and neural effects associated with feature-based attention in FEF and the inferior temporal cortex (Bichot et al., 2015) as well as V4 (Bichot et al., 2019). The authors suggested that the VPA may therefore represent a potential homolog of the human IFJ (Bichot et al., 2015). The problem of identifying homologies between species has become a hot topic in recent years, potentially due to the increase in the animal models investigated (Carlén, 2017), but also more importantly thanks to the availability of data from the same modality (MRI) across species (Mars et al., 2021; Neubert et al., 2014; Sallet et al., 2013). Using this data, it becomes possible to identify those homologies through an approach named connectivity blueprint matching (Mars et al., 2018b), which enables ‘horizontal translations’ across species (in this case, the macaque and the human PFC; Mars et al., 2021). This technique works by establishing the similarity of the connectivity profile of specific vertices by looking at the cortical terminations of white matter bundles that are present in both species. If a region receives the same bundle terminations, its organization is deemed evolutionarily preserved across species. Otherwise, if highly dissimilar, the region may have undergone some substantial changes in its connectivity that are not explained by simple expansion in size (Mars et al., 2018b). In principle therefore, by comparing the connectivity fingerprints of the IFJ with that of the VPA, and other surrounding areas in the macaque, one could be able to objectively assess what would be the most likely homolog of this area. This could be done either by matching their connectivity fingerprint with known homolog target regions (similar to Neubert et al., 2014, and Sallet et al., 2013), or by using the connectivity blueprint matching technique to evaluate whether the human ventro-lateral PFC underwent significant reorganization and relocation, or simple expansion in size.

Finally, moving beyond connectivity, the results I presented offer some ideas for interpreting the nature of the attentional template (Desimone & Duncan, 1995). In brief, how is a behaviorally relevant stimulus represented in the PFC? Some studies argue for a format that is still sensory in nature, while others suggest a more abstract representational format (reviewed in Christophel et al., 2017). This question is not only crucial for theories of attentional control but has implications for models of how the task set is implemented in the brain (Dosenbach et al., 2006; Muhle-Karbe et al., 2017). In this dissertation, I partly leaned on the interpretation that FEF and IFJ encode representations in a way that still carries some sensory information (although dissociated along the spatial and non-spatial domains), based on the divergence in their structural connections presented in chapter 4. In chapter 2 however, I also hypothesized that since the IFJ can operate at the object-based level (Baldauf & Desimone, 2014), its representations could be encoded at a more abstract level than FEF.

Recent work on neural coding in the macaque PFC indicated that for complex tasks some neural populations exhibit forms of mixed selectivity (Rigotti et al., 2013). In other words, they are able to encode multiple task-relevant properties at the same time. Single-unit and local field potential data suggest that orthogonal coding between stimuli dimensions may be advantageous as these neurons are able to maximize discriminability between overlapping task sets and facilitate readout by other neural populations (see Fusi et al., 2016 for a discussion). From this point of view, MVPA is a tool that can help disentangle different representational formats. I am excited about the opportunity to investigate whether decoding and computational modeling techniques (MVPA, and inverted encoding models) would support the idea of dissociation in spatial vs non-spatial control by collecting fMRI data using a working memory task during my visit to the University of California San Diego, where I'm presently writing this dissertation and working in the final months of my PhD.

Appendix

APPENDIX A

Tables 1 and 2 summarize the information on the subsample of studies used to carry out the ALE meta-analysis to infer the localization of the FEF and IFJ used in the surface-based probabilistic tractography analysis presented in chapter 4.

Table 1 List of the studies included in the FEF subsample

Study	N	Age	Paradigm	Contrast	Design	Eye tracker	Results reported for	N° of foci	Multiple FEF foci
Amiez and Petrides (2018)	13	22.6 ± 2.8	Functional localizer	Prosaccades > Fixation	Blocked	N	Single foci	2	N
Cameron et al. (2015)	15	20.7 ± 1.7	Functional localizer	Antisaccades & prosaccades > Fixation	<i>Event-related</i>	Y	ROIs only	8	N
Christophe et al. (2018)	22	24.4 ± 0.83	Functional localizer	Vertical & horizontal instructed saccades > Fixation	<i>Event-related</i>	N	Single foci	2	N
Duicker et al. (2013)	20	19-28	Functional localizer	Prosaccades > Fixation	Blocked	N	Single foci	2	N
Fernandez-Ruiz et al. (2018)	25	21.7 ± 1.9	Functional localizer	Correct prosaccades & antisaccades > Fixation	<i>Event-related</i>	Y	Whole-brain	18	N
Ford et al. (2005)	10	28	Oculomotor task	Late preparatory period comparison: Antisaccades > Prosaccades	<i>Event-related</i>	Y	Whole-brain	8	N
Furlan et al. (2016)	6	N/A	Functional localizer	Execution of Antisaccades & Prosaccades > Fixation	<i>Event-related</i>	Y	ROIs only	6	N
Guo et al. (2012)	12	19-31	Functional localizer	Prosaccades > Fixation	Blocked	Y	ROIs only	6	N
Gavet et al. (2018)	16	23.2	Functional localizer	Prosaccades > Fixation	Blocked	Y	Single foci	2	N
Jannard et al. (2015)	23	25.8; 18-43	Functional localizer	Antisaccades > Fixation	<i>Event-related</i>	Y	Whole-brain	47	N
Jarvstad and Gilchrist (2019)	23	N/A	Functional localizer	Prosaccades in inhibition trials > Prosaccades in selection trials	Blocked	Y	Whole-brain	4	N
Kastner et al. (2007)	4	20-36	Functional localizer	Prosaccades > Fixation	Blocked	Y	ROIs only	5	N
Krebs et al. (2010)	16	25 ± 4.6	Oculomotor task	Conditional saccades > Fixation	<i>Event-related</i>	Y	Whole-brain	15	Y
Levy et al. (2007)	8	24-43	Functional localizer	Prosaccades > Fixation	Blocked	N	ROIs only	5	N
Marmorech et al. (2007)	21	34.2 ± 12.6	Functional localizer	Antisaccade > Prosaccade	<i>Event-related</i>	Y	Whole-brain	19	N
Schon et al. (2008)	17	21.29 ± 3.72	Functional localizer	Prosaccades > Fixation	Blocked	N	Whole-brain	19	Y
Tamler-Rosenau et al. (2018)	10	28.5 ± 3.3	Functional localizer	Prosaccades > Fixation	Blocked	Y	ROIs only	6	N
Thakkar et al. (2014)	37	29.3; 19-48	Oculomotor task	Compensated > No-step saccades	<i>Event-related</i>	Y	Whole-brain	39	Y
Tibber et al. (2010)	16	21-40	Functional localizer	Endogenous & exogenous prosaccades > Fixation	Blocked	Y	ROIs only	9	N
Van Pelt et al. (2010)	18	20-37	Functional localizer	Prosaccades in darkness > Fixation	<i>Event-related</i>	Y	ROIs only	7	N
Vessel et al. (2015)	16	24.9; 19-31	Functional localizer	Cued prosaccades > Fixation	<i>Event-related</i>	Y	Whole-brain	11	N

Table 2 List of the studies included in the IFJ subsample

Study	N	Age	Paradigm	Contrast	Design	Results reported for	N° of foci
Asplund et al. (2010)	30	NA	RSVP / Oddball paradigm	Surprise > Search trials	<i>Event-related</i>	Whole-brain	4
Baldau and Desimone (2014)	12	23-37	Object-based attention paradigm	Attend face & attend house blocks > Passive view	Blocked	Single foci	2
Boilinger et al. (2010)	18	23.4 ± 3.06; 18-28	Working memory paradigm (n-back)	Functional connectivity with FFA: Stimulus known > Passive view + stimulus unknown	<i>Event-related</i>	Whole-brain	17
Cole and Schneider (2007)	9	19-42	Working memory paradigm	Target switching trials target non-occluded > Non-switching trials target non-occluded	Mixed blocked/ <i>Event-related</i>	Whole-brain	12
Derrfuss et al. (2012)	12	25.3 ± 2.4; 22-31	Snoop paradigm	Incongruent > Congruent trials	<i>Event-related</i>	ROIs only	2
Han and Marois (2013)	22	19-35	RSVP / Oddball paradigm	Discontinuous > Continuous & continuous-hard conditions	<i>Event-related</i>	Whole-brain	12
Han and Marois (2014)	14	20-32	RSVP / Oddball paradigm	Target > Distractor trials	<i>Event-related</i>	Whole-brain	11
Han and Marois (2014)	6	19-35	RSVP / Oddball paradigm	Target > Distractor trials	<i>Event-related</i>	Whole-brain	11
Han et al. (2018)	20	22-33	RSVP / Oddball paradigm	Oddball trials > Search trials	<i>Event-related</i>	ROIs only	4
Hemsefer et al. (2011)	27	24.56 ± 2.53	Covert attention / Working memory paradigm	Internal > External attending (position task)	Blocked	Whole-brain	15
Lin et al. (2019)	18	27.4 ± 6.6	Working memory paradigm (n-back)	Functional connectivity face cue > scene cue	<i>Event-related</i>	Whole-brain	9
Meeyappan et al. (2022)	20	24.65 ± 2.8	Endogenous cuing paradigm	Spatial and feature-based task cue-evoked activity	<i>Event-related</i>	Whole-brain	23
Secorivassan et al. (2014)	16	22; 18-32	Working memory paradigm	Memory > Relation discrimination trials	Blocked	Whole-brain	13
Stelzel et al. (2010)	48	F: 22 ± 1.99; M: 22.6 ± 1.99	Working memory paradigm	Task switch > Repetition trials	<i>Event-related</i>	ROIs only	2
Todd et al. (2011)	18	18-31	Working memory paradigm (n-back)	Encoding period > No-event fixation trials	<i>Event-related</i>	Whole-brain	27
Wills et al. (2017)	22	18-30	Contingent capture paradigm	Salient target > Baseline	<i>Event-related</i>	ROIs only	13
Yin et al. (2017)	26	21.3; 21-25	Task-switching paradigm	Task switch > Repetition trials	<i>Event-related</i>	Whole-brain	15
Zanto et al. (2010)	13	25; 20-31	Working memory paradigm (n-back)	Functional connectivity V5: Attend > Ignore motion	<i>Event-related</i>	Whole-brain	8
Zanto et al. (2011)	20	24.25; 18-31	Working memory paradigm (n-back)	Functional connectivity V5: Attend > Ignore motion	<i>Event-related</i>	Whole-brain	16
Zanto et al. (2014)	20	25.7	Working memory paradigm (n-back)	Functional connectivity V5: Attend > Ignore motion	<i>Event-related</i>	ROIs only	5
Zhang et al. (2018)	19	19-26	Feature-based attention paradigm	Stimulus block > Baseline	Blocked	ROIs only	8
Zhao et al. (2020)	13	21.54 ± 1.99	Working memory paradigm	High working memory load > Low working memory load	<i>Event-related</i>	Whole-brain	7

APPENDIX B**Reproducible workflow HCP-MEG subjects - CIMEC Think Open initiative**

Introduction: The MEG community has witnessed a rise in interest in implementing standard and reproducible pipelines for data analysis (Gross et al., 2013; Jas et al., 2018; Niso et al., 2018). Recently, increasing efforts have been put forward by the core developers of the main software tools available (Brainstorm, Fieldtrip, and MNE-Python) to implement and enable robust and efficient compliance with those guidelines.

Main objectives: The aim of this project was to prepare the MEG data from the HCP-MEG subjects (Larson-Prior et al., 2013; HCP_dataset) in a reproducible way to enable subsequent analyses using open-source software. First, the MEG data was converted into a format compatible with MNE-Python (v1.0.2; Gramfort et al., 2013). The next goals were to organize the data in the BIDS standard, validate this process, and use scripting tools to automatically query the dataset based on demographic information stored as file meta-data (as the sample includes 68 twins). This opens up the possibility of investigating the role of genetic contributions to resting-state connectivity patterns (for example, see Haak & Beckmann 2019). Another use case would be randomizing sample selection to exclude potential genetic confounds, as I for example did in chapter 4.

Technical implementation: I used Datalad (Halchenko et al., 2021) to access the HCP-MEG dataset from the command line through an Amazon Web Services account (see Figure 1 for an overview). Datalad leverages git-annex, a version control tool, to download an exact and synchronized copy of this dataset. Next, I created a conda virtual environment where I installed all the Python packages and dependencies required: first, MNE-HCP to convert the files into an MNE compatible format, second, MNE-BIDS (Appelhoff et al., 2019) to ‘BIDS-ify’ the data, and finally PyBIDS to query and manipulate the dataset.

Results: Although some of the MNE-Python modules employed are no longer maintained, and can be therefore at first challenging to work with, overall the integration of the computational tools reported provides an effective way to interact with the HCP-MEG data. This project offers an example of a fully reproducible and version-controlled workflow for the HCP-MEG data, from downloading, preparing, and analyzing this dataset potentially all the way to storing the results and code in a public repository.

Period of project implementation: from February 2021 to May 2021

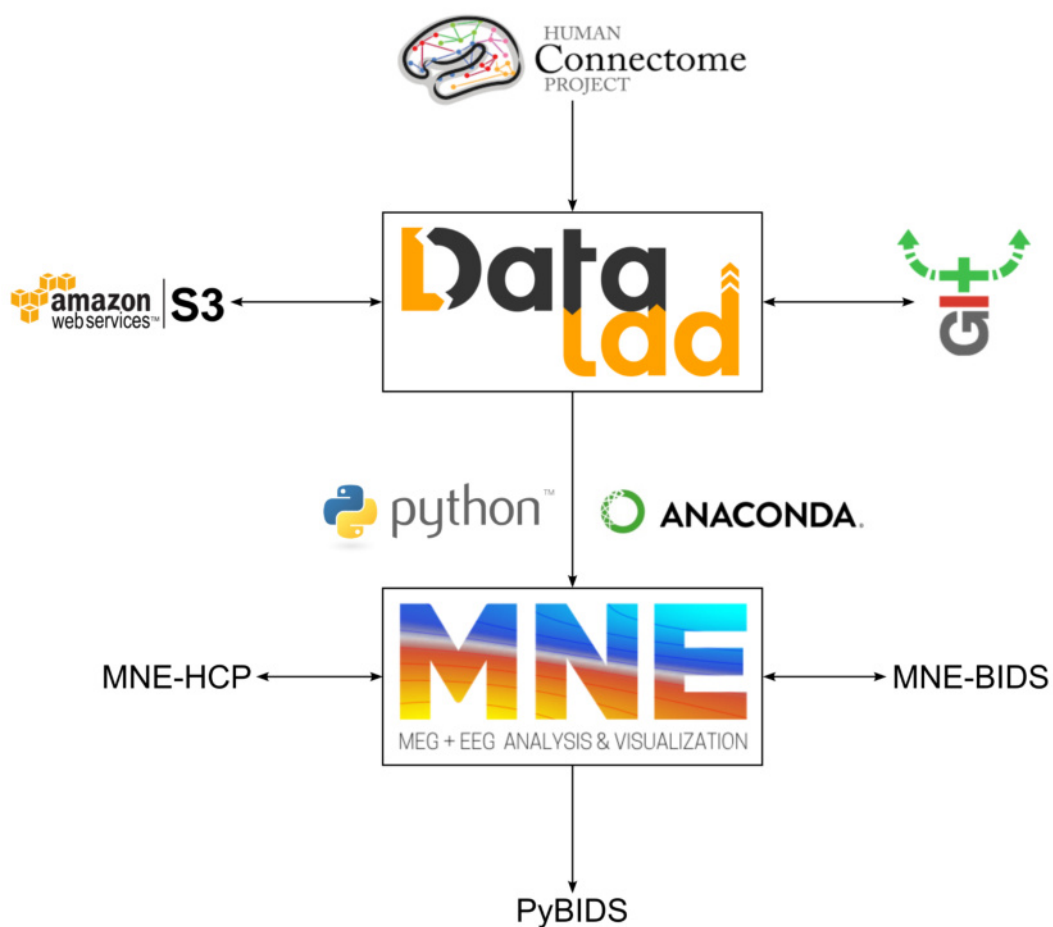


FIGURE 1 Overview of the HCP-MEG subject reproducible workflow

Links to the software and tools used for this project:

Datalad: <https://bit.ly/3SQZQcX>;

MNE-Python: <https://bit.ly/3SMf96L>;

MNE-HCP: <https://bit.ly/3Rv0A6L>;

MNE-BIDS: <https://bit.ly/3E7UiXs>;

PyBIDS: <https://bit.ly/3SvKxXp>.

I credit all the developers of these free and open source software, tools, and projects.

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I saved this bit for the end not because I think it is less important, but because I didn't want it to take precedence over the content of this dissertation. Research however doesn't happen in a vacuum and while part of my work was carried out in a rather deterritorialized way, I had the great pleasure to cross paths with many people who significantly contributed to shaping and challenging my views, from whom I could learn critical skills, collaborate on a project, or simply enjoy life (in as much as pursuing doctorate allows). Firstly, I want to thank my advisor Daniel. When I was admitted to the doctoral program, I certainly wasn't the candidate with the most impressive background and credentials to start a neuroimaging-focused project. Nevertheless, when we first discussed my project proposal, he immediately recognized our shared research interests and goals. I'm grateful that he trusted my motivation to apply myself and pursue my research objectives and for his supervision throughout the program. I feel very privileged that I had the opportunity to focus on a research line closely related to the one he worked on during his time at MIT in the Desimone lab. I thank the former students of Daniel's lab, Giorgio Marinato and Arianna Brancaccio, for how they welcomed me when I joined the lab and in the early times in Rovereto. Without meeting Giorgio, my time in Trentino would have been way less interesting and rewarding. Among many other things, I thank him in particular for introducing me to the free libre and open source software movement in relation to neuroimaging, the spontaneous discussions about all kinds of topics (where he invariably brought incredible depth), and the awesome vinyl-only sets he used to throw as a DJ. I also thank Ingmar De Vries, who joined Daniel's lab as a postdoc when I was starting the second year of my PhD. Ingmar brought an unmatched mix of expert knowledge, great energy, and genuine friendliness to our lab. Even though he ended up spending just one year in our lab, I learned a great deal from him and I very much admire how he progressed from a very successful recent PhD graduate to a rising independent researcher in our field.

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BIBLIOGRAPHY

- Abdollahi, R. O., Kolster, H., Glasser, M. F., Robinson, E. C., Coalson, T. S., Dierker, D., Jenkinson, M., Van Essen, D. C., & Orban, G. A. (2014). Correspondences between retinotopic areas and myelin maps in human visual cortex. *NeuroImage*, 99, 509–524. <https://doi.org/10.1016/j.neuroimage.2014.06.042>
- Acar, F., Seurinck, R., Eickhoff, S. B., & Moerkerke, B. (2018). Assessing robustness against potential publication bias in Activation Likelihood Estimation (ALE) meta-analyses for fMRI. *PLoS ONE*, 13(11), 1–23. <https://doi.org/10.1371/journal.pone.0208177>
- Alkan, Y., Biswal, B. B., & Alvarez, T. L. (2011). Differentiation between vergence and saccadic functional activity within the human frontal eye fields and midbrain revealed through fMRI. *PLoS ONE*, 6(11). <https://doi.org/10.1371/journal.pone.0025866>
- Allen, M., Poggiali, D., Whitaker, K., Marshall, T. R., & Kievit, R. A. (2019). Raincloud plots: A multi-platform tool for robust data visualization [version 1; peer review: 2 approved]. *Wellcome Open Research*, 4, 1–52. <https://doi.org/10.12688/wellcomeopenres.15191.1>
- Alves, P. N., Forkel, S. J., Corbetta, M., & Thiebaut de Schotten, M. (2022). The subcortical and neurochemical organization of the ventral and dorsal attention networks. *Communications Biology*, 5(1). <https://doi.org/10.1038/s42003-022-04281-0>
- Amiez, C., & Petrides, M. (2009). Anatomical organization of the eye fields in the human and non-human primate frontal cortex. *Progress in neurobiology*, 89(2), 220–230. <https://doi.org/10.1016/j.pneurobio.2009.07.010>
- Amiez, C., Kostopoulos, P., Champod, A. S., & Petrides, M. (2006). Local morphology predicts functional organization of the dorsal premotor region in the human brain. *Journal of Neuroscience*, 26(10), 2724–2731. <https://doi.org/10.1523/JNEUROSCI.4739-05.2006>
- Amiez, C., & Petrides, M. (2018). Functional rostro-caudal gradient in the human posterior lateral frontal cortex. *Brain Structure and Function*, 223(3), 1487–1499. <https://doi.org/10.1007/s00429-017-1567-z>
- Amunts, K., & von Cramon, D. Y. (2006). The anatomical segregation of the frontal cortex: what does it mean for function?. *Cortex*, 42(4), 525–528. [https://doi.org/10.1016/S0010-9452\(08\)70392-7](https://doi.org/10.1016/S0010-9452(08)70392-7)

-
- Amunts, K., & Zilles, K. (2015). Architectonic mapping of the human brain beyond Brodmann. *Neuron*, 88(6), 1086-1107. <https://doi.org/10.1016/j.neuron.2015.12.001>
- Amunts, K., Lenzen, M., Friederici, A. D., Schleicher, A., Morosan, P., Palomero-Gallagher, N., & Zilles, K. (2010). Broca's region: Novel organizational principles and Multiple Receptor Mapping. *PLoS Biology*, 8(9). <https://doi.org/10.1371/journal.pbio.1000489>
- Amunts, K., Mohlberg, H., Bludau, S., & Zilles, K. (2020). Julich-Brain: A 3D probabilistic atlas of the human brain's cytoarchitecture. *Science*, 369(6506), 988-992. <https://doi.org/10.1126/science.abb4588>
- Amunts, K., Schleicher, A., Bürgel, U., Mohlberg, H., Uylings, H. B., & Zilles, K. (1999). Broca's region revisited: cytoarchitecture and intersubject variability. *Journal of Comparative Neurology*, 412(2), 319-341. [https://doi.org/10.1002/\(SICI\)1096-9861\(19990920\)412:2<319::AID-CNE10>3.0.CO;2-7](https://doi.org/10.1002/(SICI)1096-9861(19990920)412:2<319::AID-CNE10>3.0.CO;2-7)
- Anderson, B. A. (2019). Neurobiology of value-driven attention. *Current opinion in psychology*, 29, 27-33. <https://doi.org/10.1016/j.copsyc.2018.11.004>
- Anderson, E. J., Jones, D. K., O'Gorman, R. L., Leemans, A., Catani, M., & Husain, M. (2012). Cortical network for gaze control in humans revealed using multimodal MRI. *Cerebral Cortex*, 22(4), 765-775. <https://doi.org/10.1093/cercor/bhr110>
- Andersson, J. L. R., & Sotiropoulos, S. N. (2016). An integrated approach to correction for off-resonance effects and subject movement in diffusion MR imaging. *NeuroImage*, 125, 1063–1078. <https://doi.org/10.1016/j.neuroimage.2015.10.019>
- Anzellotti, S., & Coutanche, M. N. (2018). Beyond functional connectivity: investigating networks of multivariate representations. *Trends in cognitive sciences*, 22(3), 258-269. <https://doi.org/10.1016/j.tics.2017.12.002>
- Appelhoff, S., Sanderson, M., Brooks, T., van Vliet, M., Quentin, R., Holdgraf, C., Chaumon, M., Mikulan, E., Tavabi, K., Höchenberger, R., Welke, D., Brunner, C., Rockhill, A., Larson, E., Gramfort, A., & Jas, M. (2019). MNE-BIDS: Organizing electrophysiological data into the BIDS format and facilitating their analysis. *Journal of Open Source Software*, 4(44), 1896. <https://doi.org/10.21105/joss.01896>
- Armbruster, D. J. N., Ueltzhöffer, K., Basten, U., & Fiebach, C. J. (2012). Prefrontal cortical mechanisms underlying individual differences in cognitive flexibility and stability. *Journal of Cognitive Neuroscience*, 24(12), 2385–2399. https://doi.org/10.1162/jocn_a_00286

- Asplund, C. L., Todd, J. J., Snyder, A. P., & Marois, R. (2010). A central role for the lateral prefrontal cortex in goal-directed and stimulus-driven attention. *Nature neuroscience*, 13(4), 507-512. <https://doi.org/10.1038/nn.2509>
- Assem, M., Glasser, M. F., Van Essen, D. C., & Duncan, J. (2020). A domain-general cognitive core defined in multimodally parcellated human cortex. *Cerebral Cortex*, 30(8), 4361–4380. <https://doi.org/10.1093/cercor/bhaa023>
- Assem, M., Shashidhara, S., Glasser, M. F., & Duncan, J. (2021). Precise Topology of Adjacent Domain-General and Sensory-Biased Regions in the Human Brain. *Cerebral Cortex*, October 2021, 2521–2537. <https://doi.org/10.1093/cercor/bhab362>
- Astafiev, S. V., Shulman, G. L., Stanley, C. M., Snyder, A. Z., Van Essen, D. C., & Corbetta, M. (2003). Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. *Journal of Neuroscience*, 23(11), 4689-4699. <https://doi.org/10.1523/JNEUROSCI.23-11-04689.2003>
- Atmaca, S., Stadler, W., Keitel, A., Ott, D. V. M., Lepsien, J., & Prinz, W. (2013). Prediction processes during multiple object tracking (MOT): Involvement of dorsal and ventral premotor cortices. *Brain and Behavior*, 3(6), 683–700. <https://doi.org/10.1002/brb3.180>
- Autio, J. A., Glasser, M. F., Ose, T., Donahue, C. J., Bastiani, M., Ohno, M., ... & Yamaguchi, M. (2020). Towards HCP-Style macaque connectomes: 24-Channel 3T multi-array coil, MRI sequences and preprocessing. *NeuroImage*, 215, 116800. <https://doi.org/10.1016/j.neuroimage.2020.116800>
- Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in cognitive sciences*, 5(3), 119-126. [https://doi.org/10.1016/S1364-6613\(00\)01593-X](https://doi.org/10.1016/S1364-6613(00)01593-X)
- Awh, E., Belopolsky, A. V., & Theeuwes, J. (2012). Top-down versus bottom-up attentional control: A failed theoretical dichotomy. *Trends in cognitive sciences*, 16(8), 437-443. <https://doi.org/10.1016/j.tics.2012.06.010>
- Awh, E., Jonides, J., & Reuter-Lorenz, P. A. (1998). Rehearsal in spatial working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 24(3), 780–790. <https://doi.org/10.1037/0096-1523.24.3.780>
- Baddeley, A. D. (1993). Working memory or working attention? In: Baddeley A., & Weiskrantz L. (Eds.), *Attention: Selection, awareness, and control*, (pp. 152–170). Oxford: Clarendon.

-
- Badre, D., & Nee, D. E. (2018). Frontal cortex and the hierarchical control of behavior. *Trends in Cognitive Sciences*, 22(2), 170–188. <https://doi.org/10.1016/j.tics.2017.11.005>
- Baldauf, D., & Desimone, R. (2014). Neural mechanisms of object-based attention. *Science*, 344(6182), 424–427. <https://doi.org/10.1126/science.1247003>
- Barbas, H., & Pandya, D. N. (1989). Architecture and intrinsic connections of the prefrontal cortex in the rhesus monkey. *Journal of Comparative Neurology*, 286(3), 353–375. <https://doi.org/10.1002/cne.902860306>
- Barbeau, E. B., Descoteaux, M., & Petrides, M. (2020). Dissociating the white matter tracts connecting the temporo-parietal cortical region with frontal cortex using diffusion tractography. *Scientific Reports*, 10(1), 1–13. <https://doi.org/10.1038/s41598-020-64124-y>
- Barceló, F., Suwazono, S., & Knight, R. T. (2000). Prefrontal modulation of visual processing in humans. *Nature neuroscience*, 3(4), 399–403. <https://doi.org/10.1038/73975>
- Barch DM, Burgess GC, Harms MP, et al (2013) Function in the human connectome: Task-fMRI and individual differences in behavior. *Neuroimage* 80:169–189. <https://doi.org/10.1016/j.neuroimage.2013.05.033>
- Bardi, L., Kanai, R., Mapelli, D., & Walsh, V. (2012). TMS of the FEF interferes with spatial conflict. *Journal of cognitive neuroscience*, 24(6), 1305–1313. https://doi.org/10.1162/jocn_a_00223
- Barrett, R. L. C., Dawson, M., Dyrby, T. B., Krug, K., Ptito, M., D’Arceuil, H., Croxson, P. L., Johnson, P. J., Howells, H., Forkel, S. J., Dell’Acqua, F., & Catani, M. (2020). Differences in frontal network anatomy across primate species. *Journal of Neuroscience*, 40(10), 2094–2107. <https://doi.org/10.1523/JNEUROSCI.1650-18.2019>
- Bär, S., Hauf, M., Barton, J. J. S., & Abegg, M. (2016). The neural network of saccadic foreknowledge. *Experimental Brain Research*, 234(2), 409–418. <https://doi.org/10.1007/s00221-015-4468-5>
- Bartolomeo, P., & Seidel Malkinson, T. (2019). Hemispheric lateralization of attention processes in the human brain. *Current Opinion in Psychology*, 29, 90–96. <https://doi.org/10.1016/j.copsyc.2018.12.023>
- Beauchamp MS, Petit L, Ellmore TM, et al (2001) A parametric fMRI study of overt and covert shifts of visuospatial attention. *Neuroimage* 14:310–321. <https://doi.org/10.1006/nimg.2001.0788>

- Bedini, M., & Baldauf, D. (2021). Structure, function and connectivity fingerprints of the frontal eye field versus the inferior frontal junction: A comprehensive comparison. *European Journal of Neuroscience*, 54(4), 5462-5506. <https://doi.org/10.1111/ejn.15393>
- Bedini, M.; Olivetti, E.; Avesani, P.; Baldauf, D. (2021). TALKS: Submission 84 The anatomical pathways underlying spatial versus non-spatial attention. *Cognitive Processing*, 22, 1–2. <https://doi.org/10.1007/s10339-021-01058-x>
- Behrens, T. E. J., Berg, H. J., Jbabdi, S., Rushworth, M. F. S., & Woolrich, M. W. (2007). Probabilistic diffusion tractography with multiple fibre orientations: What can we gain? *NeuroImage*, 34(1), 144–155. <https://doi.org/10.1016/j.neuroimage.2006.09.018>
- Behrens, T. E. J., Woolrich, M. W., Jenkinson, M., Johansen-Berg, H., Nunes, R. G., Clare, S., Matthews, P. M., Brady, J. M., & Smith, S. M. (2003). Characterization and Propagation of Uncertainty in Diffusion-Weighted MR Imaging. *Magnetic Resonance in Medicine*, 50(5), 1077–1088. <https://doi.org/10.1002/mrm.10609>
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal statistical society: series B (Methodological)*, 57(1), 289-300.
- Benson, N. C., Jamison, K. W., Arcaro, M. J., Vu, A. T., Glasser, M. F., Coalson, T. S., Van Essen, D. C., Yacoub, E., Ugurbil, K., Winawer, J., & Kay, K. (2018). The Human Connectome Project 7 Tesla retinotopy dataset: Description and population receptive field analysis. *Journal of Vision*, 18(13), 1–22. <https://doi.org/10.1167/18.13.23>
- Benson, N. C., Butt, O. H., Datta, R., Radoeva, P. D., Brainard, D. H., & Aguirre, G. K. (2012). The retinotopic organization of striate cortex is well predicted by surface topology. *Current Biology*, 22(21), 2081–2085. <https://doi.org/10.1016/j.cub.2012.09.014>
- Berman, R. A., Colby, C. L., Genovese, C. R., Voyvodic, J. T., Luna, B., Thulborn, K. R., & Sweeney, J. A. (1999). Cortical networks subserving pursuit and saccadic eye movements in humans: An FMRI study. *Human Brain Mapping*, 8(4), 209–225. [https://doi.org/10.1002/\(SICI\)1097-0193\(1999\)8:4<209::AID-HBM5>3.0.CO;2-0](https://doi.org/10.1002/(SICI)1097-0193(1999)8:4<209::AID-HBM5>3.0.CO;2-0)
- Bichot, N. P., Heard, M. T., DeGennaro, E. M., & Desimone, R. (2015). A Source for Feature-Based Attention in the Prefrontal Cortex. *Neuron*, 88(4), 832–844. <https://doi.org/10.1016/j.neuron.2015.10.001>

-
- Bichot, N. P., Xu, R., Ghadooshahy, A., Williams, M. L., & Desimone, R. (2019). The role of prefrontal cortex in the control of feature attention in area V4. *Nature communications*, 10(1), 1-12. <https://doi.org/10.1038/s41467-019-13761-7>
- Blanke O, Spinelli CAL, Thut G, et al (2000) Location of the human frontal eye field as defined by electrical cortical stimulation: anatomical, functional and electrophysiological characteristics. *NeuroReport* 11:1907–1913. <https://doi.org/10.1097/00001756-200006260-00021>
- Bode, S., & Haynes, J. D. (2009). Decoding sequential stages of task preparation in the human brain. *NeuroImage*, 45(2), 606–613. <https://doi.org/10.1016/j.neuroimage.2008.11.031>
- Bollinger, J., Rubens, M. T., Zanto, T. P., & Gazzaley, A. (2010). Expectation-driven changes in cortical functional connectivity influence working memory and long-term memory performance. *Journal of Neuroscience*, 30(43), 14399–14410. <https://doi.org/10.1523/JNEUROSCI.1547-10.2010>
- Botvinik-Nezer, R., Holzmeister, F., Camerer, C. F., Dreber, A., Huber, J., Johannesson, M., Kirchler, M., Iwanir, R., Mumford, J. A., Adcock, R. A., Avesani, P., Baczkowski, B. M., Bajracharya, A., Bakst, L., Ball, S., Barilari, M., Bault, N., Beaton, D., Beitner, J., ... Schonberg, T. (2020). Variability in the analysis of a single neuroimaging dataset by many teams. *Nature*, November 2019. <https://doi.org/10.1038/s41586-020-2314-9>
- Bourgeois, A., Chica, A. B., Migliaccio, R., Bayle, D. J., Duret, C., Pradat-Diehl, P., Lunven, M., Pouget, P., & Bartolomeo, P. (2015). Inappropriate rightward saccades after right hemisphere damage: Oculomotor analysis and anatomical correlates. *Neuropsychologia*, 73, 1–11. <https://doi.org/10.1016/j.neuropsychologia.2015.04.013>
- Braga, R. M., Fu, R. Z., Seemungal, B. M., Wise, R. J. S., & Leech, R. (2016). Eye movements during auditory attention predict individual differences in dorsal attention network activity. *Frontiers in Human Neuroscience*, 10(MAY2016), 1–13. <https://doi.org/10.3389/fnhum.2016.00164>
- Brass, M., & Von Cramon, D. Y. (2002). The role of the frontal cortex in task preparation. *Cerebral cortex*, 12(9), 908-914. <https://doi.org/10.1093/cercor/12.9.908>
- Brass, M., & Von Cramon, D. Y. (2004). Decomposing components of task preparation with functional magnetic resonance imaging. *Journal of Cognitive Neuroscience*, 16(4), 609–620. <https://doi.org/10.1162/089892904323057335>

- Brass, M., Derrfuss, J., Forstmann, B., & von Cramon, D. Y. (2005). The role of the inferior frontal junction area in cognitive control. *Trends in cognitive sciences*, 9(7), 314-316. <https://doi.org/10.1016/j.tics.2005.05.001>
- Brett, M., Johnsrude, I. S., & Owen, A. M. (2002). The problem of functional localization in the human brain. *Nature Reviews Neuroscience*, 3(3), 243–249. <https://doi.org/10.1038/nrn756>
- Brevers, D., Bechara, A., Cleeremans, A., & Noël, X. (2013). Iowa Gambling Task (IGT): twenty years after—gambling disorder and IGT. *Frontiers in psychology*, 4, 665. <https://doi.org/10.3389/fpsyg.2013.00665>
- Bristow, D., Haynes, J. D., Sylvester, R., Frith, C. D., & Rees, G. (2005). Blinking suppresses the neural response to unchanging retinal stimulation. *Current Biology*, 15(14), 1296-1300. <https://doi.org/10.1016/j.cub.2005.06.025>
- Brodmann, K. (1909). Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues. Barth.
- Brown, M. R. G., Goltz, H. C., Vilis, T., Ford, K. A., & Everling, S. (2006). Inhibition and generation of saccades: Rapid event-related fMRI of prosaccades, antisaccades, and nogo trials. *NeuroImage*, 33(2), 644–659. <https://doi.org/10.1016/j.neuroimage.2006.07.002>
- Brown, M. R. G., Vilis, T., & Everling, S. (2007). Frontoparietal activation with preparation for antisaccades. *Journal of Neurophysiology*, 98(3), 1751–1762. <https://doi.org/10.1152/jn.00460.2007>
- Bruce, C. J., Goldberg, M. E., Bushnell, M. C., & Stanton, G. B. (1985). Primate frontal eye fields. II. Physiological and anatomical correlates of electrically evoked eye movements. *Journal of neurophysiology*, 54(3), 714-734. <https://doi.org/10.1152/jn.1985.54.3.714>
- Bruce, C. J., & Goldberg, M. E. (1985). Primate frontal eye fields. I. Single neurons discharging before saccades. *Journal of Neurophysiology*, 53(3), 603–635. <https://doi.org/10.1152/jn.1985.53.3.603>
- Bullier, J. (2001). Integrated model of visual processing. *Brain research reviews*, 36(2-3), 96-107. [https://doi.org/10.1016/S0165-0173\(01\)00085-6](https://doi.org/10.1016/S0165-0173(01)00085-6)
- Bullock, D., Takemura, H., Caiafa, C. F., Kitchell, L., McPherson, B., Caron, B., & Pestilli, F. (2019). Associative white matter connecting the dorsal and ventral posterior human cortex. *Brain Structure and Function*, 224(8), 2631–2660. <https://doi.org/10.1007/s00429-019-01907-8>

-
- Bunge, S. A., Kahn, I., Wallis, J. D., Miller, E. K., & Wagner, A. D. (2003). Neural circuits subserving the retrieval and maintenance of abstract rules. *Journal of neurophysiology*, 90(5), 3419-3428. <https://doi.org/10.1152/jn.00910.2002>
- Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science*, 315(5820), 1860-1862. <https://doi.org/10.1126/science.1138071>
- Buschman, T. J., & Miller, E. K. (2009). Serial, covert shifts of attention during visual search are reflected by the frontal eye fields and correlated with population oscillations. *Neuron*, 63(3), 386-396. <https://doi.org/10.1016/j.neuron.2009.06.020>
- Button, K. S., Ioannidis, J. P. A., Mokrysz, C., Nosek, B. A., Flint, J., Robinson, E. S. J., & Munafò, M. R. (2013). Power failure: Why small sample size undermines the reliability of neuroscience. *Nature Reviews Neuroscience*, 14(5), 365-376. <https://doi.org/10.1038/nrn3475>
- Calamante, F. (2019). The seven deadly sins of measuring brain structural connectivity using diffusion MRI streamlines fibre-tracking. *Diagnostics*, 9(3). <https://doi.org/10.3390/diagnostics9030115>
- Cameron, I. G. M., Coe, B. C., Watanabe, M., Stroman, P. W., & Munoz, D. P. (2009). Role of the basal ganglia in switching a planned response. *European Journal of Neuroscience*, 29(12), 2413-2425. <https://doi.org/10.1111/j.1460-9568.2009.06776.x>
- Caminiti, R., Innocenti, G. M., & Battaglia-Mayer, A. (2015). Organization and evolution of parieto-frontal processing streams in macaque monkeys and humans. *Neuroscience & Biobehavioral Reviews*, 56, 73-96. <https://doi.org/10.1016/j.neubiorev.2015.06.014>
- Carlén, M. (2017). What constitutes the prefrontal cortex? *Science*, 358(6362), 478-482. <https://doi.org/10.1126/science.aan8868>
- Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, 51(13), 1484-1525. <https://doi.org/10.1016/j.visres.2011.04.012>
- Casanova, M. F., & Opris, I. (2015). Recent advances on the modular organization of the cortex. In *Recent Advances on the Modular Organization of the Cortex*. <https://doi.org/10.1007/978-94-017-9900-3>
- Catani, M., & Thiebaut de Schotten, M. (2008). A diffusion tensor imaging tractography atlas for virtual in vivo dissections. *Cortex*, 44(8), 1105-1132. <https://doi.org/10.1016/j.cortex.2008.05.004>

- Catani, M., Howard, R. J., Pajevic, S., & Jones, D. K. (2002). Virtual in Vivo interactive dissection of white matter fasciculi in the human brain. *NeuroImage*, 17(1), 77–94. <https://doi.org/10.1006/nimg.2002.1136>
- Cavada, C., & Goldman-Rakic, P. S. (1989). Posterior parietal cortex in rhesus monkey: II. Evidence for segregated corticocortical networks linking sensory and limbic areas with the frontal lobe. *Journal of Comparative Neurology*, 287(4), 422–445. <https://doi.org/10.1002/cne.902870403>
- Chacko, R. V., Kim, B., Jung, S. W., Daitch, A. L., Roland, J. L., Metcalf, N. V., ... & Leuthardt, E. C. (2018). Distinct phase-amplitude couplings distinguish cognitive processes in human attention. *NeuroImage*, 175, 111–121. <https://doi.org/10.1016/j.neuroimage.2018.03.003>
- Chafee, M. V, & Heilbronner, S. R. (2022). Prefrontal cortex. *Current Biology*, 32(8), R346–R351. <https://doi.org/10.1016/j.cub.2022.02.071>
- Chan, A. W. Y. (2013). Functional organization and visual representations of human ventral lateral prefrontal cortex. *Frontiers in Psychology*, 4, 371. <https://doi.org/10.3389/fpsyg.2013.00371>
- Chang, L., Bao, P., & Tsao, D. Y. (2017). The representation of colored objects in macaque color patches. *Nature Communications*, 8(1), 1–14. <https://doi.org/10.1038/s41467-017-01912-7>
- Chen, Z., Lei, X., Ding, C., Li, H., & Chen, A. (2013). The neural mechanisms of semantic and response conflicts: An fMRI study of practice-related effects in the Stroop task. *NeuroImage*, 66, 577–584. <https://doi.org/10.1016/j.neuroimage.2012.10.028>
- Chica, A. B., Paz-Alonso, P. M., Valero-Cabré, A., & Bartolomeo, P. (2013). Neural bases of the interactions between spatial attention and conscious perception. *Cerebral Cortex*, 23(6), 1269–1279. <https://doi.org/10.1093/cercor/bhs087>
- Christophel, T. B., Klink, P. C., Spitzer, B., Roelfsema, P. R., & Haynes, J. D. (2017). The Distributed Nature of Working Memory. *Trends in Cognitive Sciences*, 21(2), 111–124. <https://doi.org/10.1016/j.tics.2016.12.007>
- Christophel, T. B., Allefeld, C., Endisch, C., & Haynes, J. D. (2018). View-Independent Working Memory Representations of Artificial Shapes in Prefrontal and Posterior Regions of the Human Brain. *Cerebral Cortex (New York, N.Y. : 1991)*, 28(6), 2146–2161. <https://doi.org/10.1093/cercor/bhx119>
- Chun, M. M., Golomb, J. D., & Turk-Browne, N. B. (2011). A taxonomy of external and internal attention. *Annual review of psychology*, 62, 73–101. <https://doi.org/10.1146/annurev.psych.093008.100427>

-
- Cieslik, E., Seidler, I., Laird, A., Fox, P., & Eickhoff, S. (2016). Different involvement of subregions within dorsal premotor and medial frontal cortex for pro-and antisaccades. *Neuroscience and Biobehavioral Reviews*, 68, 256–269. <https://doi.org/10.1016/j.neubiorev.2016.05.012>
- Cloutman, L. L. (2013). Interaction between dorsal and ventral processing streams: Where, when and how? *Brain and Language*, 127(2), 251–263. <https://doi.org/10.1016/j.bandl.2012.08.003>
- Coalson, T. S., Van Essen, D. C., & Glasser, M. F. (2018). The impact of traditional neuroimaging methods on the spatial localization of cortical areas. *Proceedings of the National Academy of Sciences of the United States of America*, 115(27), E6356–E6365. <https://doi.org/10.1073/pnas.1801582115>
- Cole, M. W., & Schneider, W. (2007). The cognitive control network: Integrated cortical regions with dissociable functions. *NeuroImage*, 37(1), 343–360. <https://doi.org/10.1016/j.Neuroimage.2007.03.071>
- Cole, M. W., Ito, T., Bassett, D. S., & Schultz, D. H. (2016). Activity flow over resting-state networks shapes cognitive task activations. *Nature Neuroscience*, 19(12), 1718–1726. <https://doi.org/10.1038/nn.4406>
- Cole, M. W., Reynolds, J. R., Power, J. D., Repovs, G., Anticevic, A., & Braver, T. S. (2013). Multi-task connectivity reveals flexible hubs for adaptive task control. *Nature neuroscience*, 16(9), 1348–1355. <https://doi.org/10.1038/nn.3470>
- Coltheart, M. (2006). What has Functional Neuroimaging told us about the Mind (so far)? (Position Paper Presented to the European Cognitive Neuropsychology Workshop, Bressanone, 2005). *Cortex*, 42(3), 323–331. [https://doi.org/10.1016/s0010-9452\(08\)70358-7](https://doi.org/10.1016/s0010-9452(08)70358-7)
- Connolly, J. D., Goodale, M. A., Cant, J. S., & Munoz, D. P. (2007). Effector-specific fields for motor preparation in the human frontal cortex. *NeuroImage*, 34(3), 1209–1219. <https://doi.org/10.1016/j.neuroimage.2006.10.001>
- Connolly, J. D., Goodale, M. A., Desouza, J. F. X., Menon, R. S., & Vilis, T. (2000). A comparison of frontoparietal fMRI activation during anti-saccades and anti-pointing. *Journal of Neurophysiology*, 84(3), 1645–1655. <https://doi.org/10.1152/jn.2000.84.3.1645>
- Connolly, J. D., Goodale, M. A., Goltz, H. C., & Munoz, D. P. (2005). fMRI activation in the human frontal eye field is correlated with saccadic reaction time. *Journal of Neurophysiology*, 94(1), 605–611. <https://doi.org/10.1152/jn.00830.2004>

- Connolly, J. D., Goodale, M. A., Menon, R. S., & Munoz, D. P. (2002). Human fMRI evidence for the neural correlates of preparatory set. *Nature Neuroscience*, 5(12), 1345–1352. <https://doi.org/10.1038/nn969>
- Constantinidis, C., & Qi, X. L. (2018). Representation of spatial and feature information in the monkey dorsal and ventral prefrontal cortex. *Frontiers in Integrative Neuroscience*, 12, 31. <https://doi.org/10.3389/fnint.2018.00031>
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3), 201–215. <https://doi.org/10.1038/nrn755>
- Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., ... & Shulman, G. L. (1998). A common network of functional areas for attention and eye movements. *Neuron*, 21(4), 761–773. [https://doi.org/10.1016/S0896-6273\(00\)80593-0](https://doi.org/10.1016/S0896-6273(00)80593-0)
- Corbetta, M. (1998). Frontoparietal cortical networks for directing attention and the eye to visual locations: identical, independent, or overlapping neural systems?. *Proceedings of the National Academy of Sciences*, 95(3), 831–838. <https://doi.org/10.1073/pnas.95.3.831>
- Corradi-Dell'Acqua, C., Fink, G. R., & Weidner, R. (2015). Selecting category specific visual information: Top-down and bottom-up control of object based attention. *Consciousness and Cognition*, 35, 330–341. <https://doi.org/10.1016/j.concog.2015.02.006>
- Cottaar, M., Bastiani, M., Boddu, N., Glasser, M. F., Haber, S., van Essen, D. C., Sotiropoulos, S. N., & Jbabdi, S. (2021). Modelling white matter in gyral blades as a continuous vector field. *NeuroImage*, 227(December 2020), 117693. <https://doi.org/10.1016/j.neuroimage.2020.117693>
- Courtney, S. M., Petit, L., Maisog, J. M., Ungerleider, L. G., & Haxby, J. V. (1998). An area specialized for spatial working memory in human frontal cortex. *Science*, 279(5355), 1347–1351. <https://doi.org/10.1126/science.279.5355.1347>
- Croxson, P. L., Johansen-Berg, H., Behrens, T. E., Robson, M. D., Pinski, M. A., Gross, C. G., ... & Rushworth, M. F. (2005). Quantitative investigation of connections of the prefrontal cortex in the human and macaque using probabilistic diffusion tractography. *Journal of Neuroscience*, 25(39), 8854–8866. <https://doi.org/10.1523/JNEUROSCI.1311-05.2005>
- Curtis, C. E., & Sprague, T. C. (2021). Persistent Activity During Working Memory From Front to Back. *Frontiers in Neural Circuits*, 15(July), 1–17. <https://doi.org/10.3389/fncir.2021.696060>

-
- Curtis, C. E., & Connolly, J. D. (2008). Saccade preparation signals in the human frontal and parietal cortices. *Journal of Neurophysiology*, 99(1), 133–145. <https://doi.org/10.1152/jn.00899.2007>
- Daducci, A., Dal Palù, A., Lemkaddem, A., & Thiran, J. P. (2015). COMMIT: Convex optimization modeling for microstructure informed tractography. *IEEE Transactions on Medical Imaging*, 34(1), 246–257. <https://doi.org/10.1109/TMI.2014.2352414>
- de Haan, E. H. F., Jackson, S. R., & Schenk, T. (2018). Where are we now with ‘What’ and ‘How’? *Cortex*, 98, 1–7. <https://doi.org/10.1016/j.cortex.2017.12.001>
- de Haan, B., Morgan, P. S., & Rorden, C. (2008). Covert orienting of attention and overt eye movements activate identical brain regions. *Brain Research*, 1204, 102–111. <https://doi.org/10.1016/j.brainres.2008.01.105>
- Dell'Acqua, F., Scifo, P., Rizzo, G., Catani, M., Simmons, A., Scotti, G., & Fazio, F. (2010). A modified damped Richardson–Lucy algorithm to reduce isotropic background effects in spherical deconvolution. *Neuroimage*, 49(2), 1446–1458. <https://doi.org/10.1016/j.neuroimage.2009.09.033>
- De Pasquale, F., Della Penna, S., Snyder, A. Z., Lewis, C., Mantini, D., Marzetti, L., ... & Corbetta, M. (2010). Temporal dynamics of spontaneous MEG activity in brain networks. *Proceedings of the National Academy of Sciences*, 107(13), 6040–6045. <https://doi.org/10.1073/pnas.0913863107>
- Derrfuss, J., Brass, M., & Von Cramon, D. Y. (2004). Cognitive control in the posterior frontolateral cortex: evidence from common activations in task coordination, interference control, and working memory. *Neuroimage*, 23(2), 604–612. <https://doi.org/10.1016/j.neuroimage.2004.06.007>
- Derrfuss, J., Brass, M., Neumann, J., & von Cramon, D. Y. (2005). Involvement of the inferior frontal junction in cognitive control: Meta-analyses of switching and Stroop studies. *Human brain mapping*, 25(1), 22–34. <https://doi.org/10.1002/hbm.20127>
- Derrfuss, J., Brass, M., von Cramon, D. Y., Lohmann, G., & Amunts, K. (2009). Neural activations at the junction of the inferior frontal sulcus and the inferior precentral sulcus: interindividual variability, reliability, and association with sulcal morphology. *Human brain mapping*, 30(1), 299–311. <https://doi.org/10.1002/hbm.20501>
- Derrfuss, J., Vogt, V. L., Fiebach, C. J., Von Cramon, D. Y., & Tittgemeyer, M. (2012). Functional organization of the left inferior precentral sulcus: Dissociating the inferior frontal eye field and the inferior frontal junction. *NeuroImage*, 59(4), 3829–3837. <https://doi.org/10.1016/j.neuroimage.2011.11.051>

- de Schotten, M. T., & Forkel, S. J. (2022). The emergent properties of the connected brain. *Science*, 378(6619), 505–510. <https://doi.org/10.1126/science.abq2591>
- de Schotten, M. T., Dell'Acqua, F., Forkel, S. J., Simmons, A., Vergani, F., Murphy, D. G., & Catani, M. (2011). A lateralized brain network for visuospatial attention. *Nature Neuroscience*, 14(10), 1245–1247. <https://doi.org/10.1038/npre.2011.5549.1>
- de Schotten, M. T., Dell'Acqua, F., Valabregue, R., & Catani, M. (2012). Monkey to human comparative anatomy of the frontal lobe association tracts. *Cortex*, 48(1), 82–96. <https://doi.org/10.1016/j.cortex.2011.10.001>
- Desikan, R. S., Ségonne, F., Fischl, B., Quinn, B. T., Dickerson, B. C., Blacker, D., Buckner, R. L., Dale, A. M., Maguire, R. P., Hyman, B. T., Albert, M. S., & Killiany, R. J. (2006). An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. *NeuroImage*. <https://doi.org/10.1016/j.neuroimage.2006.01.021>
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18(1), 193–222. <https://doi.org/10.1146/annurev.ne.18.030195.001205>
- DeSouza, J. F. X., & Everling, S. (2002). Neural correlates for preparatory set associated with pro-saccades and anti-saccades in humans investigated with event-related fMRI. *Journal of Vision*, 2(7), 1016–1023. <https://doi.org/10.1167/2.7.578>
- Destrieux, C., Fischl, B., Dale, A., & Halgren, E. (2010). Automatic parcellation of human cortical gyri and sulci using standard anatomical nomenclature. *NeuroImage*, 53(1), 1–15. <https://doi.org/10.1016/j.neuroimage.2010.06.010>
- Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision research*, 36(12), 1827–1838. [https://doi.org/10.1016/0042-6989\(95\)00294-4](https://doi.org/10.1016/0042-6989(95)00294-4)
- Donahue, C. J., Glasser, M. F., Preuss, T. M., Rilling, J. K., & Van Essen, D. C. (2018). Quantitative assessment of prefrontal cortex in humans relative to nonhuman primates. *Proceedings of the National Academy of Sciences*, 115(22), E5183–E5192. <https://doi.org/10.1073/pnas.1721653115>
- Donahue, C. J., Sotiropoulos, S. N., Jbabdi, S., Hernandez-Fernandez, M., Behrens, T. E., Dyrby, T. B., Coalson, T., Kennedy, H., Knoblauch, K., Van Essen, D. C., & Glasser, M. F. (2016). Using Diffusion Tractography to Predict Cortical Connection Strength and Distance: A Quantitative Comparison with Tracers in the Monkey. *The Journal of Neuroscience*, 36(25), 6758–6770. <https://doi.org/10.1523/JNEUROSCI.0493-16.2016>

-
- Doricchi, F., Thiebaut de Schotten, M., Tomaiuolo, F., & Bartolomeo, P. (2008). White matter (dis)connections and gray matter (dys)functions in visual neglect: Gaining insights into the brain networks of spatial awareness. *Cortex*, 44(8), 983–995. <https://doi.org/10.1016/j.cortex.2008.03.006>
- Dosenbach, N. U. F., Visscher, K. M., Palmer, E. D., Miezin, F. M., Wenger, K. K., Kang, H. C., Burgund, E. D., Grimes, A. L., Schlaggar, B. L., & Petersen, S. E. (2006). A Core System for the Implementation of Task Sets. *Neuron*, 50(5), 799–812. <https://doi.org/10.1016/j.neuron.2006.04.031>
- Duecker, F., Formisano, E., & Sack, A. T. (2013). Hemispheric differences in the voluntary control of spatial attention: direct evidence for a right-hemispheric dominance within frontal cortex. *Journal of Cognitive Neuroscience*, 25(8), 1332–1342. <https://doi.org/10.1162/jocn>
- Dumoulin, S. O., & Wandell, B. A. (2008). Population receptive field estimates in human visual cortex. *Neuroimage*, 39(2), 647–660. <https://doi.org/10.1016/j.neuroimage.2007.09.034>
- Duncan, J. (2001). An adaptive coding model of neural function in prefrontal cortex. *Nature Reviews Neuroscience*, 2(11), 820–829. <https://doi.org/10.1038/35097575>
- Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. *Trends in Cognitive Sciences*, 14(4), 172–179. <https://doi.org/10.1016/j.tics.2010.01.004>
- Dux, P. E., Ivanoff, J., Asplund, C. L., & Marois, R. (2006). Isolation of a Central Bottleneck of Information Processing with Time-Resolved fMRI. *Neuron*, 52(6), 1109–1120. <https://doi.org/10.1016/j.neuron.2006.11.009>
- D’Andrea, A., Chella, F., Marshall, T. R., Pizzella, V., Romani, G. L., Jensen, O., & Marzetti, L. (2019). Alpha and alpha-beta phase synchronization mediate the recruitment of the visuospatial attention network through the Superior Longitudinal Fasciculus. *NeuroImage*, 188(March 2018), 722–732. <https://doi.org/10.1016/j.neuroimage.2018.12.056>
- Eichert, N., Robinson, E. C., Bryant, K. L., Jbabdi, S., Jenkinson, M., Li, L., ... & Mars, R. B. (2020). Cross-species cortical alignment identifies different types of anatomical reorganization in the primate temporal lobe. *Elife*, 9, e53232. <https://doi.org/10.7554/eLife.53232.sa2>
- Eichert, N., Verhagen, L., Folloni, D., Jbabdi, S., Khrapitchev, A. A., Sibson, N. R., Mantini, D., Sallet, J., & Mars, R. B. (2019). What is special about the human arcuate fasciculus? Lateralization, projections, and expansion. *Cortex*, 118, 107–115. <https://doi.org/10.1016/j.cortex.2018.05.005>

- Eickhoff, S. B., Bzdok, D., Laird, A. R., Kurth, F., & Fox, P. T. (2012). Activation likelihood estimation meta-analysis revisited. *Neuroimage*, 59(3), 2349-2361. <https://doi.org/10.1016/j.neuroimage.2011.09.017>
- Eickhoff, S. B., Constable, R. T., & Yeo, B. T. (2018a). Topographic organization of the cerebral cortex and brain cartography. *Neuroimage*, 170, 332-347. <https://doi.org/10.1016/j.neuroimage.2017.02.018>
- Eickhoff, S. B., Nichols, T. E., Laird, A. R., Hoffstaedter, F., Amunts, K., Fox, P. T., Bzdok, D., & Eickhoff, C. R. (2016). Behavior, sensitivity, and power of activation likelihood estimation characterized by massive empirical simulation. *NeuroImage*, 137, 70–85. <https://doi.org/10.1016/j.neuroimage.2016.04.072>
- Eickhoff, S. B., Yeo, B. T. T., & Genon, S. (2018b). Imaging-based parcellations of the human brain. *Nature Reviews Neuroscience*, 19(11), 672–686. <https://doi.org/10.1038/s41583-018-0071-7>
- Eickhoff, S. B., Laird, A. R., Fox, P. M., Lancaster, J. L., & Fox, P. T. (2017). Implementation errors in the GingerALE Software: Description and recommendations. *Human Brain Mapping*, 38(1), 7–11. <https://doi.org/10.1002/hbm.23342>
- Eickhoff, S. B., Laird, A. R., Grefkes, C., Wang, L. E., Zilles, K., & Fox, P. T. (2009). Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: A random-effects approach based on empirical estimates of spatial uncertainty. *Human brain mapping*, 30(9), 2907-2926. <https://doi.org/10.1002/hbm.20718>
- Eklund, A., Nichols, T. E., & Knutsson, H. (2016). Cluster failure: Why fMRI inferences for spatial extent have inflated false-positive rates. *Proceedings of the national academy of sciences*, 113(28), 7900-7905. <https://doi.org/10.1073/pnas.1602413113>
- Elam, J. S., Glasser, M. F., Harms, M. P., Sotiropoulos, S. N., Andersson, J. L. R., Burgess, G. C., Curtiss, S. W., Oostenveld, R., Larson-Prior, L. J., Schoffelen, J.-M., Hodge, M. R., Cler, E. A., Marcus, D. M., Barch, D. M., Yacoub, E., Smith, S. M., Ugurbil, K., & Van Essen, D. C. (2021). The Human Connectome Project: A retrospective. *NeuroImage*, 244(May), 118543. <https://doi.org/10.1016/j.neuroimage.2021.118543>
- Fan, L., Li, H., Zhuo, J., Zhang, Y., Wang, J., Chen, L., Yang, Z., Chu, C., Xie, S., Laird, A. R., Fox, P. T., Eickhoff, S. B., Yu, C., & Jiang, T. (2016). The Human Brainnetome Atlas: A New Brain Atlas Based on Connectional Architecture. *Cerebral Cortex*, 26(8), 3508–3526. <https://doi.org/10.1093/cercor/bhw157>

-
- Fan, J., Mccandliss, T. B. D., Fossella, J., Flombaum, J. I., & Posner, M. I. (2005). *The activation of attentional networks*. 26, 471–479. <https://doi.org/10.1016/j.neuroimage.2005.02.004>
- Fecteau, J. H., & Munoz, D. P. (2006). Salience, relevance, and firing: a priority map for target selection. *Trends in cognitive sciences*, 10(8), 382–390. <https://doi.org/10.1016/j.tics.2006.06.011>
- Fedorenko, E., Duncan, J., & Kanwisher, N. (2012). Language-selective and domain-general regions lie side by side within Broca's area. *Current Biology*, 22(21), 2059–2062. <https://doi.org/10.1016/j.cub.2012.09.011>
- Fedorenko, E., Duncan, J., & Kanwisher, N. (2013). Broad domain generality in focal regions of frontal and parietal cortex. *Proceedings of the National Academy of Sciences*, 110(41), 16616–16621. <https://doi.org/10.1073/pnas.1315235110>
- Fedorenko, E. (2021). The early origins and the growing popularity of the individual-subject analytic approach in human neuroscience. *Current Opinion in Behavioral Sciences*, 40, 105–112. <https://doi.org/10.1016/j.cobeha.2021.02.023>
- Felleman, D. J., & Van Essen, D. C. (1991). Distributed Hierarchical Processing in the Primate Cerebral Cortex. *Cerebral Cortex*, 1(1), 1–47. <http://dx.doi.org/10.1093/cercor/1.1.1>
- Fernández-Miranda, J. C., Wang, Y., Pathak, S., Stefaneau, L., Verstynen, T., & Yeh, F. C. (2015). Asymmetry, connectivity, and segmentation of the arcuate fascicle in the human brain. *Brain Structure and Function*, 220(3), 1665–1680. <https://doi.org/10.1007/s00429-014-0751-7>
- Fernandez-Ruiz, J., Peltsch, A., Alahyane, N., Brien, D. C., Coe, B. C., Garcia, A., & Munoz, D. P. (2018). Age related prefrontal compensatory mechanisms for inhibitory control in the antisaccade task. *NeuroImage*, 165(October 2017), 92–101. <https://doi.org/10.1016/j.neuroimage.2017.10.001>
- Ferrier, D. (1875). Experiments on the brain of monkeys. No. I. *Proceedings of the Royal Society of London*, 23(156–163), 409–430. <https://doi.org/10.1098/rspl.1874.0058>
- Ferrier, D., & Yeo, G. F. (1884). XIX. A record of experiments on the effects of lesion of different regions of the cerebral hemispheres. *Philosophical Transactions of the Royal Society of London*, (175), 479–564.
- Fiebelkorn, I. C., & Kastner, S. (2019). A rhythmic theory of attention. *Trends in cognitive sciences*, 23(2), 87–101. <https://doi.org/10.1016/j.tics.2018.11.009>

- Fiebelkorn, I. C., & Kastner, S. (2020). Functional specialization in the attention network. *Annual review of psychology*, 71, 221–249. <https://doi.org/10.1146/annurev-psych-010418-103429>
- Fischl, B., Rajendran, N., Busa, E., Augustinack, J., Hinds, O., Yeo, B. T. T., Mohlberg, H., Amunts, K., & Zilles, K. (2008). Cortical folding patterns and predicting cytoarchitecture. *Cerebral Cortex*, 18(8), 1973–1980. <https://doi.org/10.1093/cercor/bhm225>
- Fischl, B., Sereno, M. I., Tootell, R. B. H., & Dale, A. M. (1999). High-resolution intersubject averaging and a coordinate system for the cortical surface. *Human Brain Mapping*, 8(4), 272–284. [https://doi.org/10.1002/\(SICI\)1097-0193\(1999\)8:4<272::AID-HBM10>3.0.CO;2-4](https://doi.org/10.1002/(SICI)1097-0193(1999)8:4<272::AID-HBM10>3.0.CO;2-4)
- Foerster, O. (1931). The cerebral cortex in man. *Lancet*, 2, 309–312.
- Fonov, V., Evans, A., McKinstry, R., Almli, C., & Collins, D. (2009). Unbiased nonlinear average age-appropriate brain templates from birth to adulthood. *NeuroImage*, 47, S102. [https://doi.org/10.1016/s1053-8119\(09\)70884-5](https://doi.org/10.1016/s1053-8119(09)70884-5)
- Ford, K. A., Goltz, H. C., Brown, M. R. G., & Everling, S. (2005). Neural processes associated with antisaccade task performance investigated with event-related fMRI. *Journal of Neurophysiology*, 94(1), 429–440. <https://doi.org/10.1152/jn.00471.2004>
- Fox, P. T., Laird, A. R., Fox, S. P., Fox, P. M., Uecker, A. M., Crank, M., Koenig, S. F., & Lancaster, J. L. (2005). BrainMap taxonomy of experimental design: Description and evaluation. *Human Brain Mapping*, 25(1), 185–198. <https://doi.org/10.1002/hbm.20141>
- Fox, P. T., Lancaster, J. L., Laird, A. R., & Eickhoff, S. B. (2014). Meta-analysis in human neuroimaging: Computational modeling of large-scale databases. *Annual Review of Neuroscience*, 37, 409–434. <https://doi.org/10.1146/annurev-neuro-062012-170320>
- Fox, P. T., & Lancaster, J. L. (2002). Mapping context and content: The BrainMap model. *Nature Reviews Neuroscience*, 3(4), 319–321. <https://doi.org/10.1038/nrn789>
- Fransson, P., Flodin, P., Seimyr, G. Ö., & Pansell, T. (2014). Slow fluctuations in eye position and resting-state functional magnetic resonance imaging brain activity during visual fixation. *European Journal of Neuroscience*, 40(12), 3828–3835. <https://doi.org/10.1111/ejn.12745>
- Friederici, A. D. (2011). The brain basis of language processing: From structure to function. *Physiological Reviews*, 91(4), 1357–1392. <https://doi.org/10.1152/physrev.00006.2011>

-
- Fries, P. (2005). A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. *Trends in cognitive sciences*, 9(10), 474-480. <https://doi.org/10.1016/j.neuron.2015.09.034>
- Fries, P. (2015). Rhythms for Cognition: Communication through Coherence. *Neuron*, 88(1), 220–235. <https://doi.org/10.1016/j.neuron.2015.09.034>
- Frost, M. A., & Goebel, R. (2012). Measuring structural-functional correspondence: Spatial variability of specialised brain regions after macro-anatomical alignment. *NeuroImage*, 59(2), 1369–1381. <https://doi.org/10.1016/j.neuroimage.2011.08.035>
- Funahashi, S., Bruce, C. J., & Goldman-Rakic, P. S. (1989). Mnemonic coding of visual space in the monkey's dorsolateral prefrontal cortex. *Journal of Neurophysiology*, 61(2), 331–349. <https://doi.org/10.1152/jn.1989.61.2.331>
- Furlan, M., Smith, A. T., & Walker, R. (2016). An fMRI investigation of preparatory set in the human cerebral cortex and superior colliculus for pro- and anti-saccades. *PLoS ONE*, 11(7), 1–25. <https://doi.org/10.1371/journal.pone.0158337>
- Fusi, S., Miller, E. K., & Rigotti, M. (2016). Why neurons mix: High dimensionality for higher cognition. *Current Opinion in Neurobiology*, 37, 66–74. <https://doi.org/10.1016/j.conb.2016.01.010>
- Fuster, J. M., & Alexander, G. E. (1971). Neuron activity related to short-term memory. *Science*, 173(3997), 652-654. <https://doi.org/10.1126/science.173.3997.652>
- Fuster, J. M. (2001). The prefrontal cortex—An update: Time is of the essence. *Neuron*, 30(2), 319–333. [https://doi.org/10.1016/s0896-6273\(01\)00285-9](https://doi.org/10.1016/s0896-6273(01)00285-9)
- Gaspelin, N., & Luck, S. J. (2018). The role of inhibition in avoiding distraction by salient stimuli. *Trends in cognitive sciences*, 22(1), 79-92. <https://doi.org/10.1016/j.tics.2017.11.001>
- Gazzaley, A., & Nobre, A. C. (2012). Top-down modulation: Bridging selective attention and working memory. *Trends in Cognitive Sciences*, 16(2), 129–135. <https://doi.org/10.1016/j.tics.2011.11.014>
- Gazzaley, A., Rissman, J., & D'esposito, M. (2004). Functional connectivity during working memory maintenance. *Cognitive, Affective, & Behavioral Neuroscience*, 4(4), 580-599. <https://doi.org/10.3758/CABN.4.4.580>
- Gerbella, M., Belmalih, A., Borra, E., Rozzi, S., & Luppino, G. (2010). Cortical connections of the macaque caudal ventrolateral prefrontal areas 45A and 45B. *Cerebral Cortex*, 20(1), 141–168. <https://doi.org/10.1093/cercor/bhp087>
- Germann, J., & Petrides, M. (2020). The Ventral Part of Dorsolateral Frontal Area 8A Regulates Visual Attentional Selection and the Dorsal Part Auditory Attentional

- Selection. *Neuroscience*, 441, 209-216.
<https://doi.org/10.1016/j.neuroscience.2020.05.057>
- Germann, J., Robbins, S., Halsband, U., & Petrides, M. (2005). Precentral sulcal complex of the human brain: Morphology and statistical probability maps. *Journal of Comparative Neurology*, 493(3), 334–356. <https://doi.org/10.1002/cne.20820>
- Geyer S. (2004). The microstructural border between the motor and the cognitive domain in the human cerebral cortex. *Advances in anatomy, embryology, and cell biology*, 174, I–89. <https://doi.org/10.1007/978-3-642-18910-4>
- Giesbrecht, B., Woldorff, M. G., Song, A. W., & Mangun, G. R. (2003). Neural mechanisms of top-down control during spatial and feature attention. *Neuroimage*, 19(3), 496-512. [https://doi.org/10.1016/S1053-8119\(03\)00162-9](https://doi.org/10.1016/S1053-8119(03)00162-9)
- Girard, G., Whittingstall, K., Deriche, R., & Descoteaux, M. (2014). Towards quantitative connectivity analysis: Reducing tractography biases. *NeuroImage*, 98, 266–278. <https://doi.org/10.1016/j.neuroimage.2014.04.074>
- Glasser, M. F., Coalson, T. S., Robinson, E. C., Hacker, C. D., Harwell, J., Yacoub, E., Ugurbil, K., Andersson, J., Beckmann, C. F., Jenkinson, M., Smith, S. M., & Van Essen, D. C. (2016). A multi-modal parcellation of human cerebral cortex. *Nature*, 536(7615), 171–178. <https://doi.org/10.1038/nature18933>
- Goldman-Rakic, P. S. (1996). The prefrontal landscape: Implications of functional architecture for understanding human mentation and the central executive. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 351(1346), 1445–1453. <https://doi.org/10.1098/rstb.1996.0129>
- Gong, M., & Liu, T. (2020). Biased neural representation of feature-based attention in the human frontoparietal network. *Journal of Neuroscience*, 40(43), 8386–8395. <https://doi.org/10.1523/JNEUROSCI.0690-20.2020>
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in neurosciences*, 15(1), 20. [https://doi.org/10.1016/0166-2236\(92\)90344-8](https://doi.org/10.1016/0166-2236(92)90344-8)
- Gordon, E. M., Laumann, T. O., Adeyemo, B., Huckins, J. F., Kelley, W. M., & Petersen, S. E. (2016). Generation and Evaluation of a Cortical Area Parcellation from Resting-State Correlations. *Cerebral Cortex*, 26(1), 288–303. <https://doi.org/10.1093/cercor/bhu239>
- Gorgolewski, K. J., Varoquaux, G., Rivera, G., Schwarz, Y., Ghosh, S. S., Maumet, C., Sochat, V. V., Nichols, T. E., Poldrack, R. A., Poline, J. B., Yarkoni, T., & Margulies, D. S. (2015). NeuroVault.Org: A web-based repository for collecting

-
- and sharing unthresholded statistical maps of the human brain. *Frontiers in Neuroinformatics*, 9(APR), 1–9. <https://doi.org/10.3389/fninf.2015.00008>
- Greenberg, A. S., Esterman, M., Wilson, D., Serences, J. T., & Yantis, S. (2010). Control of spatial and feature-based attention in frontoparietal cortex. *Journal of Neuroscience*, 30(43), 14330–14339. <https://doi.org/10.1523/JNEUROSCI.4248-09.2010>
- Greenberg, A. S., Verstynen, T., Chiu, Y. C., Yantis, S., Schneider, W., & Behrmann, M. (2012). Visuotopic cortical connectivity underlying attention revealed with white-matter tractography. *Journal of Neuroscience*, 32(8), 2773–2782. <https://doi.org/10.1523/JNEUROSCI.5419-11.2012>
- Gregoriou, G. G., Gotts, S. J., Zhou, H., & Desimone, R. (2009). High-frequency, long-range coupling between prefrontal and visual cortex during attention. *Science*, 324(5931), 1207–1210. <https://doi.org/10.1126/science.1171402>
- Grisot, G., Haber, S. N., & Yendiki, A. (2021). Diffusion MRI and anatomic tracing in the same brain reveal common failure modes of tractography. *NeuroImage*, 239(June), 118300. <https://doi.org/10.1016/j.neuroimage.2021.118300>
- Grosbras, M. H., Laird, A. R., & Paus, T. (2005). Cortical regions involved in eye movements, shifts of attention, and gaze perception. *Human Brain Mapping*, 25(1), 140–154. <https://doi.org/10.1002/hbm.20145>
- Grosbras, M. H. (2016). Patterns of activity in the human frontal and parietal cortex differentiate large and small saccades. *Frontiers in Integrative Neuroscience*, 10(OCT2016), 1–11. <https://doi.org/10.3389/fnint.2016.00034>
- Gross, J., Baillet, S., Barnes, G. R., Henson, R. N., Hillebrand, A., Jensen, O., Jerbi, K., Litvak, V., Maess, B., Oostenveld, R., Parkkonen, L., Taylor, J. R., van Wassenhove, V., Wibral, M., & Schoffelen, J. M. (2013). Good practice for conducting and reporting MEG research. *NeuroImage*, 65, 349–363. <https://doi.org/10.1016/j.neuroimage.2012.10.001>
- Gross, J. (2019). Primer Magnetoencephalography in Cognitive Neuroscience : A Primer. *Neuron*, 104(2), 189–204. <https://doi.org/10.1016/j.neuron.2019.07.001>
- Guo, F., Preston, T. J., Das, K., Giesbrecht, B., & Eckstein, M. P. (2012). Feature-independent neural coding of target detection during search of natural scenes. *Journal of Neuroscience*, 32(28), 9499–9510. <https://doi.org/10.1523/JNEUROSCI.5876-11.2012>
- Gurel, S. C., Castelo-Branco, M., Sack, A. T., & Duecker, F. (2018). Assessing the Functional Role of Frontal Eye Fields in Voluntary and Reflexive Saccades Using

- Continuous Theta Burst Stimulation. *Frontiers in Neuroscience*, 12(December), 1–11. <https://doi.org/10.3389/fnins.2018.00944>
- Haak, K. V., & Beckmann, C. F. (2019). Plasticity versus stability across the human cortical visual connectome. *Nature Communications*, 10(1). <https://doi.org/10.1038/s41467-019-11113-z>
- Haber, S. N., Liu, H., Seidlitz, J., & Bullmore, E. (2022). Prefrontal connectomics: from anatomy to human imaging. *Neuropsychopharmacology*, 47(1), 20–40. <https://doi.org/10.1038/s41386-021-01156-6>
- Hagler, D. J., & Sereno, M. I. (2006). Spatial maps in frontal and prefrontal cortex. *NeuroImage*, 29(2), 567–577. <https://doi.org/10.1016/j.neuroimage.2005.08.058>
- Hagmann, P., Cammoun, L., Gigandet, X., Meuli, R., Honey, C. J., Van Welden, J., & Sporns, O. (2008). Mapping the structural core of human cerebral cortex. *PLoS Biology*, 6(7), 1479–1493. <https://doi.org/10.1371/journal.pbio.0060159>
- Haile, T. M., Bohon, K. S., Romero, M. C., & Conway, B. R. (2019). Visual stimulus-driven functional organization of macaque prefrontal cortex. *NeuroImage*, 188(November 2018), 427–444. <https://doi.org/10.1016/j.neuroimage.2018.11.060>
- Hakvoort Schwerdtfeger, R. M., Alahyane, N., Brien, D. C., Coe, B. C., Stroman, P. W., & Munoz, D. P. (2013). Preparatory neural networks are impaired in adults with attention-deficit/hyperactivity disorder during the antisaccade task. *NeuroImage: Clinical*, 2(1), 63–78. <https://doi.org/10.1016/j.nicl.2012.10.006>
- Halassa, M. M., & Kastner, S. (2017). Thalamic functions in distributed cognitive control. *Nature neuroscience*, 20(12), 1669–1679. <https://doi.org/10.1038/s41593-017-0020-1>
- Halchenko, Y., Meyer, K., Poldrack, B., Solanky, D., Wagner, A., Gors, J., MacFarlane, D., Pustina, D., Sochat, V., Ghosh, S., Mönch, C., Markiewicz, C., Waite, L., Shlyakhter, I., de la Vega, A., Hayashi, S., Häusler, C., Poline, J.-B., Kadelka, T., ... Hanke, M. (2021). DataLad: distributed system for joint management of code, data, and their relationship. *Journal of Open Source Software*, 6(63), 3262. <https://doi.org/10.21105/joss.03262>
- Han, S. W., & Marois, R. (2014). Functional fractionation of the stimulus-driven attention network. *Journal of Neuroscience*, 34(20), 6958–6969. <https://doi.org/10.1523/JNEUROSCI.4975-13.2014>
- Han, S. W., & Marois, R. (2013). Dissociation between process-based and data-based limitations for conscious perception in the human brain. *NeuroImage*, 64(1), 399–406. <https://doi.org/10.1016/j.neuroimage.2012.09.016>

-
- Han, S. W., Shin, H., Jeong, D., Jung, S., Bae, E., Kim, J. Y., Baek, H. M., & Kim, K. (2018). Neural substrates of purely endogenous, self-regulatory control of attention. *Scientific Reports*, 8(1). <https://doi.org/10.1038/s41598-018-19508-6>
- Hanes, D. P., Patterson, W. F., & Schall, J. D. (1998). Role of frontal eye fields in countermanding saccades: Visual, movement, and fixation activity. *Journal of Neurophysiology*, 79(2), 817–834. <https://doi.org/10.1152/jn.1998.79.2.817>
- Harding, I. H., Harrison, B. J., Breakspear, M., Pantelis, C., & Yücel, M. (2016). Cortical Representations of Cognitive Control and Working Memory Are Dependent Yet Non-Interacting. *Cerebral Cortex*, 26(2), 557–565. <https://doi.org/10.1093/cercor/bhu208>
- Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, 293(5539), 2425–2430. <https://doi.org/10.1126/science.1063736>
- Haxby, J. V. (2012). Multivariate pattern analysis of fMRI: The early beginnings. *NeuroImage*, 62(2), 852–855. <https://doi.org/10.1016/j.neuroimage.2012.03.016>
- Hayashi, T., Hou, Y., Glasser, M. F., Autio, J. A., Knoblauch, K., Inoue-Murayama, M., Coalson, T., Yacoub, E., Smith, S., Kennedy, H., & Van Essen, D. C. (2021). The nonhuman primate neuroimaging and neuroanatomy project. *NeuroImage*, 229(December 2020), 117726. <https://doi.org/10.1016/j.neuroimage.2021.117726>
- Haynes, J. D., & Rees, G. (2006). Decoding mental states from brain activity in humans. *Nature Reviews Neuroscience*, 7(7), 523–534. <https://doi.org/10.1038/nrn1931>
- Hecht, E. E., Gutman, D. A., Bradley, B. A., Preuss, T. M., & Stout, D. (2015). Virtual dissection and comparative connectivity of the superior longitudinal fasciculus in chimpanzees and humans. *Neuroimage*, 108, 124–137. <https://doi.org/10.1016/j.neuroimage.2014.12.039>
- Heinen, S. J., Rowland, J., Lee, B. T., & Wade, A. R. (2006). An oculomotor decision process revealed by functional magnetic resonance imaging. *Journal of Neuroscience*, 26(52), 13515–13522. <https://doi.org/10.1523/JNEUROSCI.4243-06.2006>
- Heinzle, J., Hepp, K., & Martin, K. A. C. (2007). A Microcircuit Model of the Frontal Eye Fields. *Journal of Neuroscience*, 27(35), 9341–9353. <https://doi.org/10.1523/JNEUROSCI.0974-07.2007>
- Heinzle, J., Kahnt, T., & Haynes, J. D. (2011). Topographically specific functional connectivity between visual field maps in the human brain. *NeuroImage*, 56(3), 1426–1436. <https://doi.org/10.1016/j.neuroimage.2011.02.077>

- Henderson, M., & Serences, J. T. (2019). Human frontoparietal cortex represents behaviorally relevant target status based on abstract object features. *Journal of neurophysiology*, 121(4), 1410-1427. <https://doi.org/10.1152/jn.00015.2019>
- Henseler, I., Krüger, S., Dechent, P., & Gruber, O. (2011). A gateway system in rostral PFC? Evidence from biasing attention to perceptual information and internal representations. *NeuroImage*, 56(3), 1666–1676. <https://doi.org/10.1016/j.neuroimage.2011.02.056>
- Hernandez-Fernandez, M., Reguly, I., Jbabdi, S., Giles, M., Smith, S., & Sotiropoulos, S. N. (2019). Using GPUs to accelerate computational diffusion MRI: From microstructure estimation to tractography and connectomes. *NeuroImage*, 188(November 2018), 598–615. <https://doi.org/10.1016/j.neuroimage.2018.12.015>
- Herrick, R., Olsen, T., McKay, M., House, M., Hileman, M., Reid, E., Harwell, J., ... Van Essen, D. C. (2013). Human Connectome Project informatics: Quality control, database services, and data visualization. *NeuroImage*, 80, 202–219. <https://doi.org/10.1016/j.neuroimage.2013.05.077>
- Hinds, O., Polimeni, J. R., Rajendran, N., Balasubramanian, M., Amunts, K., Zilles, K., Schwartz, E. L., Fischl, B., & Triantafyllou, C. (2009). Locating the functional and anatomical boundaries of human primary visual cortex. *NeuroImage*, 46(4), 915–922. <https://doi.org/10.1016/j.neuroimage.2009.03.036>
- Hinds, O. P., Rajendran, N., Polimeni, J. R., Augustinack, J. C., Wiggins, G., Wald, L. L., Diana Rosas, H., Potthast, A., Schwartz, E. L., & Fischl, B. (2008). Accurate prediction of V1 location from cortical folds in a surface coordinate system. *NeuroImage*, 39(4), 1585–1599. <https://doi.org/10.1016/j.neuroimage.2007.10.033>
- Hippmann, B., Kuhlemann, I., Bäumer, T., Bahlmann, J., Münte, T. F., & Jessen, S. (2019). Boosting the effect of reward on cognitive control using TMS over the left IFJ. *Neuropsychologia*, 125, 109-115. <https://doi.org/10.1016/j.neuropsychologia.2019.01.016>
- Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception & psychophysics*, 57(6), 787-795. <https://doi.org/10.3758/BF03206794>
- Huang, C. C., Rolls, E. T., Feng, J., & Lin, C. P. (2022). An extended Human Connectome Project multimodal parcellation atlas of the human cortex and subcortical areas. *Brain Structure and Function*, 227(3), 763–778. <https://doi.org/10.1007/s00429-021-02421-6>
- Hubl, D., Nyffeler, T., Wurtz, P., Chaves, S., Pflugshaupt, T., Lüthi, M., ... & Müri, R. M. (2008). Time course of blood oxygenation level-dependent signal response after

-
- theta burst transcranial magnetic stimulation of the frontal eye field. *Neuroscience*, 151(3), 921–928. <https://doi.org/10.1016/j.neuroscience.2007.10.049>
- Hupé, J. M., Bordier, C., & Dojat, M. (2012). A BOLD signature of eyeblinks in the visual cortex. *Neuroimage*, 61(1), 149–161. <https://doi.org/10.1016/j.neuroimage.2012.03.001>
- Hutton, S. B., & Ettinger, U. (2006). The antisaccade task as a research tool in psychopathology: A critical review. *Psychophysiology*, 43(3), 302–313. <https://doi.org/10.1111/j.1469-8986.2006.00403.x>
- Ikkai, A., & Curtis, C. E. (2008). Cortical activity time locked to the shift and maintenance of spatial attention. *Cerebral Cortex*, 18(6), 1384–1394. <https://doi.org/10.1093/cercor/bhm171>
- Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience*, 2(3), 194–203. <https://doi.org/10.1038/35058500>
- Jamadar, S. D., Fielding, J., & Egan, G. F. (2013). Quantitative meta-analysis of fMRI and PET studies reveals consistent activation in fronto-striatal-parietal regions and cerebellum during antisaccades and prosaccades. *Frontiers in Psychology*, 4(OCT), 1–15. <https://doi.org/10.3389/fpsyg.2013.00749>
- Jamadar, S. D., Johnson, B. P., Clough, M., Egan, G. F., & Fielding, J. (2015). Behavioral and neural plasticity of ocular motor control: Changes in performance and fmri activity following antisaccade training. *Frontiers in Human Neuroscience*, 9(DEC), 1–13. <https://doi.org/10.3389/fnhum.2015.00653>
- Jarvstad, A., & Gilchrist, I. D. (2019). Cognitive control of saccadic selection and inhibition from within the core cortical saccadic network. *Journal of Neuroscience*, 39(13), 2497–2508. <https://doi.org/10.1523/JNEUROSCI.1419-18.2018>
- Jas, M., Larson, E., Engemann, D. A., Leppäkangas, J., Taulu, S., Hämäläinen, M., & Gramfort, A. (2018). A reproducible MEG/EEG group study with the MNE software: Recommendations, quality assessments, and good practices. *Frontiers in Neuroscience*, 12(AUG), 1–18. <https://doi.org/10.3389/fnins.2018.00530>
- JASP Team (2023). JASP (Version 0.17.1)[Computer software].
- Jbabdi, S., & Johansen-Berg, H. (2011). Tractography: Where Do We Go from Here? *Brain Connectivity*, 1(3), 169–183. <https://doi.org/10.1089/brain.2011.0033>
- Jbabdi, S., Lehman, J. F., Haber, S. N., & Behrens, T. E. (2013a). Human and Monkey Ventral Prefrontal Fibers Use the Same Organizational Principles to Reach Their Targets: Tracing versus Tractography. *Journal of Neuroscience*, 33(7), 3190–3201. <https://doi.org/10.1523/JNEUROSCI.2457-12.2013>

- Jbabdi, S., Sotiropoulos, S. N., & Behrens, T. E. (2013b). The topographic connectome. *Current Opinion in Neurobiology*, 23(2), 207–215. <https://doi.org/10.1016/j.conb.2012.12.004>
- Jbabdi, S., Sotiropoulos, S. N., Haber, S. N., Van Essen, D. C., & Behrens, T. E. (2015). Measuring macroscopic brain connections in vivo. *Nature Neuroscience*, 18(11), 1546–1555. <https://doi.org/10.1038/nn.4134>
- Jbabdi, S., Sotiropoulos, S. N., Savio, A. M., Graña, M., & Behrens, T. E. J. (2012). Model-based analysis of multishell diffusion MR data for tractography: How to get over fitting problems. *Magnetic Resonance in Medicine*, 68(6), 1846–1855. <https://doi.org/10.1002/mrm.24204>
- Jenkinson, M., Beckmann, C. F., Behrens, T. E., Woolrich, M. W., & Smith, S. M. (2012). Fsl. *Neuroimage*, 62(2), 782–790. <https://doi.org/10.1016/j.neuroimage.2011.09.015>
- Jerde, T. A., Merriam, E. P., Riggall, A. C., Hedges, J. H., & Curtis, C. E. (2012). Prioritized maps of space in human frontoparietal cortex. *Journal of Neuroscience*, 32(48), 17382–17390. <https://doi.org/10.1523/JNEUROSCI.3810-12.2012>
- Jeurissen, B., Descoteaux, M., Mori, S., & Leemans, A. (2019). Diffusion MRI fiber tractography of the brain. *NMR in Biomedicine*, 32(4), e3785. <https://doi.org/10.1002/nbm.3785>
- Ji, J. L., Spronk, M., Kulkarni, K., Repovš, G., Anticevic, A., & Cole, M. W. (2019). Mapping the human brain's cortical-subcortical functional network organization. *Neuroimage*, 185, 35–57. <https://doi.org/10.1016/j.neuroimage.2018.10.006>
- Johansen-Berg, H., & Behrens, T. E. (Eds.). (2013). Diffusion MRI: from quantitative measurement to in vivo neuroanatomy. Academic Press.
- Juch, H., Zimine, I., Seghier, M. L., Lazeyras, F., & Fasel, J. H. D. (2005). Anatomical variability of the lateral frontal lobe surface: Implication for intersubject variability in language neuroimaging. *NeuroImage*, 24(2), 504–514. <https://doi.org/10.1016/j.neuroimage.2004.08.037>
- Kamitani, Y., & Tong, F. (2005). Decoding the visual and subjective contents of the human brain. *Nature Neuroscience*, 8(5), 679–685. <https://doi.org/10.1038/nn1444>
- Kanwisher, N. (2010). Functional specificity in the human brain: A window into the functional architecture of the mind. *Proceedings of the National Academy of Sciences of the United States of America*, 107(25), 11163–11170. <https://doi.org/10.1073/pnas.1005062107>

-
- Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual review of neuroscience*, 23, 315-341. <https://doi.org/10.1146/annurev.neuro.23.1.315>.
- Kastner, S., & Ungerleider, L. G. (2001). The neural basis of biased competition in human visual cortex. *Neuropsychologia*, 39(12), 1263–1276. [https://doi.org/10.1016/S0028-3932\(01\)00116-6](https://doi.org/10.1016/S0028-3932(01)00116-6)
- Kastner, S., DeSimone, K., Konen, C. S., Szczepanski, S. M., Weiner, K. S., & Schneider, K. A. (2007). Topographic maps in human frontal cortex revealed in memory-guided saccade and spatial working-memory tasks. *Journal of Neurophysiology*, 97(5), 3494–3507. <https://doi.org/10.1152/jn.00010.2007>
- Kato, M., & Miyauchi, S. (2003). Human precentral cortical activation patterns during saccade tasks: an fMRI comparison with activation during intentional eyeblink tasks. *Neuroimage*, 19(4), 1260-1272. [https://doi.org/10.1016/S1053-8119\(03\)00223-4](https://doi.org/10.1016/S1053-8119(03)00223-4)
- Kim, S. Y., Kim, M. S., & Chun, M. M. (2005). Concurrent working memory load can reduce distraction. *Proceedings of the National Academy of Sciences*, 102(45), 16524-16529. <https://doi.org/10.1073/pnas.0505454102>
- Kim, C., Cilles, S. E., Johnson, N. F., & Gold, B. T. (2012). Domain general and domain preferential brain regions associated with different types of task switching: A Meta-Analysis. *Human Brain Mapping*, 33(1), 130–142. <https://doi.org/10.1002/hbm.21199>
- Kim, C., Johnson, N. F., & Gold, B. T. (2012). Common and distinct neural mechanisms of attentional switching and response conflict. *Brain Research*, 1469, 92–102. <https://doi.org/10.1016/j.brainres.2012.06.013>
- Kiyonaga, A., & Egner, T. (2013). Working memory as internal attention: Toward an integrative account of internal and external selection processes. *Psychonomic bulletin & review*, 20(2), 228-242. <https://doi.org/10.3758/s13423-012-0359-y>
- Kleinnijenhuis, M., van Mourik, T., Norris, D. G., Ruiter, D. J., van Cappellen van Walsum, A. M., & Barth, M. (2015). Diffusion tensor characteristics of gyrencephaly using high resolution diffusion MRI in vivo at 7T. *NeuroImage*, 109, 378–387. <https://doi.org/10.1016/j.neuroimage.2015.01.001>
- Koechlin, E., Ody, C., & Kouneiher, F. (2003). The architecture of cognitive control in the human prefrontal cortex. *Science*, 302 (5648), 1181–1185. <https://doi.org/10.1126/science.1088545>

- Kötter, R. (2004). Online retrieval, processing, and visualization of primate connectivity data from the CoCoMac database. *Neuroinformatics*, 2(2), 127-144. <https://doi.org/10.1385/NI:2:2:127>
- Kowler, E., Anderson, E., Doshier, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision research*, 35(13), 1897-1916. [https://doi.org/10.1016/0042-6989\(94\)00279-U](https://doi.org/10.1016/0042-6989(94)00279-U)
- Koyama, M., Hasegawa, I., Osada, T., Adachi, Y., Nakahara, K., & Miyashita, Y. (2004). Functional magnetic resonance imaging of macaque monkeys performing visually guided saccade tasks: comparison of cortical eye fields with humans. *Neuron*, 41(5), 795-807. [https://doi.org/10.1016/S0896-6273\(04\)00047-9](https://doi.org/10.1016/S0896-6273(04)00047-9)
- Kravitz, D. J., Saleem, K. S., Baker, C. I., & Mishkin, M. (2011). A new neural framework for visuospatial processing. *Nature Reviews Neuroscience*, 12(4), 217-230. <https://doi.org/10.1038/nrn3008>
- Kravitz, D. J., Saleem, K. S., Baker, C. I., Ungerleider, L. G., & Mishkin, M. (2013). The ventral visual pathway: An expanded neural framework for the processing of object quality. *Trends in Cognitive Sciences*, 17(1), 26-49. <https://doi.org/10.1016/j.tics.2012.10.011>
- Kurata, J., Thulborn, K. R., & Firestone, L. L. (2005). The cross-modal interaction between pain-related and saccade-related cerebral activation: A preliminary study by event-related functional magnetic resonance imaging. *Anesthesia and Analgesia*, 101(2), 449-456. <https://doi.org/10.1213/01.ANE.0000158468.84424.5D>
- Lafer-Sousa, R., Conway, B. R., & Kanwisher, N. G. (2016). Color-biased regions of the ventral visual pathway lie between face- and place-selective regions in humans, as in macaques. *Journal of Neuroscience*, 36(5), 1682-1697. <https://doi.org/10.1523/JNEUROSCI.3164-15.2016>
- Lancaster, J. L., Tordesillas-Gutiérrez, D., Martínez, M., Salinas, F., Evans, A., Zilles, K., ... & Fox, P. T. (2007). Bias between MNI and Talairach coordinates analyzed using the ICBM-152 brain template. *Human brain mapping*, 28(11), 1194-1205. <https://doi.org/10.1002/hbm.20345>
- Lancaster, J. L., Laird, A. R., Eickhoff, S. B., Martínez, M. J., Mickle Fox, P., & Fox, P. T. (2012). Automated regional behavioral analysis for human brain images. *Frontiers in Neuroinformatics*, 6(JULY 2012), 1-12. <https://doi.org/10.3389/fninf.2012.00023>
- Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Freitas, C. S., Rainey, L., Kochunov, P. V., Nickerson, D., Mikiten, S. A., & Fox, P. T. (2000). Automated Talairach Atlas labels for functional brain mapping. *Human Brain Mapping*, 10(3),

120–131.

[https://doi.org/10.1002/1097-0193\(200007\)10:3<120::AID-HBM30>3.0.CO;2-8](https://doi.org/10.1002/1097-0193(200007)10:3<120::AID-HBM30>3.0.CO;2-8)

Langner, R., Camilleri, J.A. (2021). Meta-Analytic Connectivity Modelling (MACM): A Tool for Assessing Region-Specific Functional Connectivity Patterns in Task-Constrained States. In: Diwadkar, V.A., B. Eickhoff, S. (eds) *Brain Network Dysfunction in Neuropsychiatric Illness*. Springer, Cham. https://doi.org/10.1007/978-3-030-59797-9_5

Langner, R., Rottschy, C., Laird, A. R., Fox, P. T., & Eickhoff, S. B. (2014). Meta-analytic connectivity modeling revisited: Controlling for activation base rates. *NeuroImage*, 99, 559–570. <https://doi.org/10.1016/j.neuroimage.2014.06.007>

LaRocque, J. J., Lewis-Peacock, J. A., Drysdale, A. T., Oberauer, K., & Postle, B. R. (2013). Decoding attended information in short-term memory: An EEG study. *Journal of Cognitive Neuroscience*, 25(1), 127–142. https://doi.org/10.1162/jocn_a_00305

Larson-Prior, L. J., Oostenveld, R., Della Penna, S., Michalareas, G., Prior, F., Babajani-Feremi, A., Schoffelen, J. M., Marzetti, L., de Pasquale, F., Di Pompeo, F., Stout, J., Woolrich, M., Luo, Q., Buehl, R., Fries, P., Pizzella, V., Romani, G. L., Corbetta, M., & Snyder, A. Z. (2013). Adding dynamics to the Human Connectome Project with MEG. *NeuroImage*, 80, 190–201. <https://doi.org/10.1016/j.neuroimage.2013.05.056>

Lawrence, B. M., Myerson, J., & Abrams, R. A. (2004). Interference with spatial working memory: An eye movement is more than a shift of attention. *Psychonomic Bulletin & Review*, 11, 488–494. <https://doi.org/10.3758/BF03196600>

Lefco, R. W., Brissenden, J. A., Noyce, A. L., Tobyn, S. M., & Somers, D. C. (2020). Gradients of functional organization in posterior parietal cortex revealed by visual attention, visual short-term memory, and intrinsic functional connectivity: Functional gradients in posterior parietal cortex. *NeuroImage*, 219(June), 117029. <https://doi.org/10.1016/j.neuroimage.2020.117029>

Lepsien, J., Thornton, I., & Nobre, A. C. (2011). Modulation of working-memory maintenance by directed attention. *Neuropsychologia*, 49, 1569–1577. <https://doi.org/10.1016/j.neuropsychologia.2011.03.011>

Levy, B. J., & Wagner, A. D. (2011). Cognitive control and right ventrolateral prefrontal cortex: Reflexive reorienting, motor inhibition, and action updating. *Annals of the New York Academy of Sciences*, 1224(1), 40–62. <https://doi.org/10.1111/j.1749-6632.2011.05958.x>

- Levy, I., Schluppeck, D., Heeger, D. J., & Glimcher, P. W. (2007). Specificity of human cortical areas for reaches and saccades. *Journal of Neuroscience*, 27(17), 4687–4696. <https://doi.org/10.1523/JNEUROSCI.0459-07.2007>
- Lin, H., Li, W. P., & Carlson, S. (2019). A privileged working memory state and potential top-down modulation for faces, not scenes. *Frontiers in Human Neuroscience*, 13. <https://doi.org/10.3389/fnhum.2019.00002>
- Liu, T., & Hou, Y. (2013). A hierarchy of attentional priority signals in human frontoparietal cortex. *Journal of Neuroscience*, 33(42), 16606–16616. <https://doi.org/10.1523/JNEUROSCI.1780-13.2013>
- Liu, T., Hospadaruk, L., Zhu, D. C., & Gardner, J. L. (2011). Feature-specific attentional priority signals in human cortex. *Journal of Neuroscience*, 31(12), 4484–4495. <https://doi.org/10.1523/JNEUROSCI.5745-10.2011>
- Liu, T., Slotnick, S. D., Serences, J. T., & Yantis, S. (2003). Cortical Mechanisms of Feature-based Attentional Control. *Cerebral Cortex*, 13(12), 1334–1343. <https://doi.org/10.1093/cercor/bhg080>
- Liu, T. (2016). Neural representation of object-specific attentional priority. *Neuroimage*, 129, 15–24. <https://doi.org/10.1016/j.neuroimage.2016.01.034>
- Lowe, K. A., & Schall, J. D. (2018). Functional categories of visuomotor neurons in macaque frontal eye field. *ENeuro*, 5(5). <https://doi.org/10.1523/ENEURO.0131-18.2018>
- Lowet, E., Gomes, B., Srinivasan, K., Zhou, H., Schafer, R. J., & Desimone, R. (2018). Enhanced neural processing by covert attention only during microsaccades directed toward the attended stimulus. *Neuron*, 99(1), 207–214. <https://doi.org/10.1016/j.neuron.2018.05.041>
- Luna, B., Thulborn, K. R., Strojwas, M. H., McCurtain, B. J., Berman, R. A., Genovese, C. R., & Sweeney, J. A. (1998). Dorsal cortical regions subserving visually guided saccades in humans: An fMRI study. *Cerebral Cortex*, 8(1), 40–47. <https://doi.org/10.1093/cercor/8.1.40>
- Luria, A.R. (1966). Higher Cortical Functions in Man. (New York: Basic Books).
- Macaluso, E., & Doricchi, F. (2013). Attention and predictions: control of spatial attention beyond the endogenous-exogenous dichotomy. *Frontiers in human neuroscience*, 7, 685. <https://doi.org/10.3389/fnhum.2013.00685>
- Mackey, W. E., Winawer, J., & Curtis, C. E. (2017). Visual field map clusters in human frontoparietal cortex. *ELife*, 6, 1–23. <https://doi.org/10.7554/eLife.22974>

-
- Maier-Hein, K. H., Neher, P. F., Houde, J. C., Côté, M. A., Garyfallidis, E., Zhong, J., ... & Reddick, W. E. (2017). The challenge of mapping the human connectome based on diffusion tractography. *Nature communications*, 8(1), 1-13. <https://doi.org/10.1038/s41467-017-01285-x>
- Manoach, D. S., Thakkar, K. N., Cain, M. S., Polli, F. E., Edelman, J. A., Fischl, B., & Barton, J. J. S. (2007). Neural activity is modulated by trial history: A functional magnetic resonance imaging study of the effects of a previous antisaccade. *Journal of Neuroscience*, 27(7), 1791–1798. <https://doi.org/10.1523/JNEUROSCI.3662-06.2007>
- Mao, L., Zhou, B., Zhou, W., & Han, S. (2007). Neural correlates of covert orienting of visual spatial attention along vertical and horizontal dimensions. *Brain Research*, 1136(1), 142–153. <https://doi.org/10.1016/j.brainres.2006.12.031>
- Markett, S., Nothdurfter, D., Focsa, A., Reuter, M., & Jawinski, P. (2021). Attention networks and the intrinsic network structure of the human brain. *Human Brain Mapping*, November, 1–18. <https://doi.org/10.1002/hbm.25734>
- Markiewicz, C. J., Gorgolewski, K. J., Feingold, F., Blair, R., Halchenko, Y. O., Miller, E., Hardcastle, N., Wexler, J., Esteban, O., Goncalves, M., Jwa, A., & Poldrack, R. (2021). The openneuro resource for sharing of neuroscience data. *ELife*, 10, 1–17. <https://doi.org/10.7554/eLife.71774>
- Markov, N. T., Ercsey-Ravasz, M. M., Ribeiro Gomes, A. R., Lamy, C., Magrou, L., Vezoli, J., ... & Sallet, J. (2014). A weighted and directed interareal connectivity matrix for macaque cerebral cortex. *Cerebral cortex*, 24(1), 17-36. <https://doi.org/10.1093/cercor/bhs270>
- Mars, R. B., Jbabdi, S., & Rushworth, M. F. S. (2021). A Common Space Approach to Comparative Neuroscience. *Annual Review of Neuroscience*, 44(1), 69–86. <https://doi.org/10.1146/annurev-neuro-100220-025942>
- Mars, R. B., Jbabdi, S., Sallet, J., O'Reilly, J. X., Croxson, P. L., Olivier, E., Noonan, M. P., Bergmann, C., Mitchell, A. S., Baxter, M. G., Behrens, T. E. J., Johansen-Berg, H., Tomassini, V., Miller, K. L., & Rushworth, M. F. S. (2011). Diffusion-Weighted Imaging Tractography-Based Parcellation of the Human Parietal Cortex and Comparison with Human and Macaque Resting-State Functional Connectivity. *Journal of Neuroscience*, 31(11), 4087–4100. <https://doi.org/10.1523/JNEUROSCI.5102-10.2011>
- Mars, R. B., Passingham, R. E., & Jbabdi, S. (2018a). Connectivity Fingerprints: From Areal Descriptions to Abstract Spaces. *Trends in Cognitive Sciences*, 22(11), 1026–1037. <https://doi.org/10.1016/j.tics.2018.08.009>

- Mars, R. B., Sotiropoulos, S. N., Passingham, R. E., Sallet, J., Verhagen, L., Khrapitchev, A. A., Sibson, N., & Jbabdi, S. (2018b). Whole brain comparative anatomy using connectivity blueprints. *ELife*, 7, 1–15. <https://doi.org/10.7554/eLife.35237>
- Marshall, T. R., Bergmann, T. O., & Jensen, O. (2015a). Frontoparietal Structural Connectivity Mediates the Top-Down Control of Neuronal Synchronization Associated with Selective Attention. *PLoS Biology*, 13(10), 1–17. <https://doi.org/10.1371/journal.pbio.1002272>
- Marshall, T. R., O'Shea, J., Jensen, O., & Bergmann, T. O. (2015b). Frontal eye fields control attentional modulation of alpha and gamma oscillations in contralateral occipitoparietal cortex. *Journal of Neuroscience*, 35(4), 1638–1647. <https://doi.org/10.1523/JNEUROSCI.3116-14.2015>
- Martin, A. B., Yang, X., Saalmann, Y. B., Wang, L., Shestyuk, A., Lin, J. J., ... & Kastner, S. (2019). Temporal dynamics and response modulation across the human visual system in a spatial attention task: An ECoG study. *Journal of Neuroscience*, 39(2), 333–352. <https://doi.org/10.1523/JNEUROSCI.1889-18.2018>
- Martinez-Trujillo, J. (2022). Visual Attention in the Prefrontal Cortex. *Annual Review of Vision Science*, 8, 407–425. <https://doi.org/10.1146/annurev-vision-100720-031711>
- Maunsell, J. H. R. (2015). Neuronal Mechanisms of Visual Attention. *Annual Review of Vision Science*, 1(1), 373–391. <https://doi.org/10.1146/annurev-vision-082114-035431>
- McDowell, J. E., Dyckman, K. A., Austin, B. P., & Clementz, B. A. (2008). Neurophysiology and neuroanatomy of reflexive and volitional saccades: Evidence from studies of humans. *Brain and Cognition*, 68(3), 255–270. <https://doi.org/10.1016/j.bandc.2008.08.016>
- McLaughlin, N. C. R., & Malloy, P. (2018). Dorsolateral Prefrontal Cortex. In *Encyclopedia of Clinical Neuropsychology*. https://doi.org/10.1007/978-3-319-57111-9_1887
- Melcher, T., & Gruber, O. (2006). Oddball and incongruity effects during Stroop task performance: A comparative fMRI study on selective attention. *Brain Research*, 1121(1), 136–149. <https://doi.org/10.1016/j.brainres.2006.08.120>
- Mendoza-Halliday, D., & Martinez-Trujillo, J. C. (2017). Neuronal population coding of perceived and memorized visual features in the lateral prefrontal cortex. *Nature communications*, 8(1), 1–13. <https://doi.org/10.1038/ncomms15471>

-
- Menon, V., & D'Esposito, M. (2022). The role of PFC networks in cognitive control and executive function. *Neuropsychopharmacology*, 47(1), 90–103. <https://doi.org/10.1038/s41386-021-01152-w>
- Mesulam, M. M. (1998). From sensation to cognition. *Brain*, 121(6), 1013–1052. <https://doi.org/10.1093/brain/121.6.1013>
- Meyer, T., Qi, X. L., & Constantinidis, C. (2007). Persistent discharges in the prefrontal cortex of monkeys naive to working memory tasks. *Cerebral Cortex*, 17(suppl_1), i70–i76. <https://doi.org/10.1093/cercor/bhm063>
- Meyer, T., Qi, X. L., Stanford, T. R., & Constantinidis, C. (2011). Stimulus selectivity in dorsal and ventral prefrontal cortex after training in working memory tasks. *Journal of Neuroscience*, 31(17), 6266–6276. <https://doi.org/10.1523/JNEUROSCI.6798-10.2011>
- Meyyappan, S., Rajan, A., Mangun, G. R., & Ding, M. (2021). Role of inferior frontal junction (IFJ) in the control of feature versus spatial attention. *Journal of Neuroscience*, 41(38), 8065–8074. <https://doi.org/10.1523/JNEUROSCI.2883-20.2021>
- Michalareas, G., Vezoli, J., Van Pelt, S., Schoffelen, J. M., Kennedy, H., & Fries, P. (2016). Alpha-beta and gamma rhythms subserve feedback and feedforward influences among human visual cortical areas. *Neuron*, 89(2), 384–397. <https://doi.org/10.1016/j.neuron.2015.12.018>
- Michalka, S. W., Kong, L., Rosen, M. L., Shinn-Cunningham, B. G., & Somers, D. C. (2015). Short-Term Memory for Space and Time Flexibly Recruit Complementary Sensory-Biased Frontal Lobe Attention Networks. *Neuron*, 87(4), 882–892. <https://doi.org/10.1016/j.neuron.2015.07.028>
- Milham, M. P., Ai, L., Koo, B., Xu, T., Amiez, C., Balezeau, F., ... & Croxson, P. L. (2018). An open resource for non-human primate imaging. *Neuron*, 100(1), 61–74. <https://doi.org/10.1016/j.neuron.2018.08.039>
- Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual review of neuroscience*, 24(1), 167–202. <https://doi.org/10.1146/annurev.neuro.24.1.167>
- Miller, K. L., Stagg, C. J., Douaud, G., Jbabdi, S., Smith, S. M., Behrens, T. E. J., Jenkinson, M., Chance, S. A., Esiri, M. M., Voets, N. L., Jenkinson, N., Aziz, T. Z., Turner, M. R., Johansen-Berg, H., & McNab, J. A. (2011). Diffusion imaging of whole, post-mortem human brains on a clinical MRI scanner. *NeuroImage*, 57(1), 167–181. <https://doi.org/10.1016/j.neuroimage.2011.03.070>

- Miller, J. A., Voorhies, W. I., Lurie, D. J., D'Esposito, M., & Weiner, K. S. (2021). Overlooked tertiary sulci serve as a meso-scale link between microstructural and functional properties of human lateral prefrontal cortex. *The Journal of Neuroscience*, 41(10), JN-RM-2362-20. <https://doi.org/10.1523/jneurosci.2362-20.2021>
- Mills, K. (2016). HCP-MMP1.0 projected on fsaverage. <https://doi.org/10.6084/m9.figshare.3498446.v2>
- Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: Two cortical pathways. *Trends in Neurosciences*, 6, 414–417. [https://doi.org/10.1016/0166-2236\(83\)90190-X](https://doi.org/10.1016/0166-2236(83)90190-X)
- Mitchell, A. S. (2015). The mediodorsal thalamus as a higher order thalamic relay nucleus important for learning and decision-making. *Neuroscience and Biobehavioral Reviews*, 54, 76–88. <https://doi.org/10.1016/j.neubiorev.2015.03.001>
- Mohanty, A., Egner, T., Monti, J. M., & Mesulam, M. M. (2009). Search for a threatening target triggers limbic guidance of spatial attention. *Journal of Neuroscience*, 29(34), 10563–10572. <https://doi.org/10.1523/JNEUROSCI.1170-09.2009>
- Movahedian Attar, F., Kirilina, E., Haenelt, D., Pine, K. J., Trampel, R., Edwards, L. J., & Weiskopf, N. (2020). Mapping Short Association Fibers in the Early Cortical Visual Processing Stream Using in Vivo Diffusion Tractography. *Cerebral Cortex*, 30(8), 4496–4514. <https://doi.org/10.1093/cercor/bhaa049>
- Moore, T., & Armstrong, K. M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. *Nature*, 421(6921), 370–373. <https://doi.org/10.1038/nature01341>
- Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Sciences*, 98(3), 1273–1276. <https://doi.org/10.1073/pnas.98.3.1273>
- Moore, T., & Zirnsak, M. (2015). The what and where of visual attention. *Neuron*, 88(4), 626–628. <https://doi.org/10.1016/j.neuron.2015.11.005>
- Moore, T., & Zirnsak, M. (2017). Neural mechanisms of selective visual attention. *Annual review of psychology*, 68, 47–72. <https://doi.org/10.1146/annurev-psych-122414-033400>
- Muhle-Karbe, P. S., Andres, M., & Brass, M. (2014). Transcranial magnetic stimulation dissociates prefrontal and parietal contributions to task preparation. *Journal of Neuroscience*, 34(37), 12481–12489. <https://doi.org/10.1523/JNEUROSCI.4931-13.2014>

-
- Muhle-Karbe, P. S., Derrfuss, J., Lynn, M. T., Neubert, F. X., Fox, P. T., Brass, M., & Eickhoff, S. B. (2016). Co-activation-based parcellation of the lateral prefrontal cortex delineates the inferior frontal junction area. *Cerebral cortex*, 26(5), 2225-2241. <https://doi.org/10.1093/cercor/bhv073>
- Muhle-Karbe, P. S., Duncan, J., De Baene, W., Mitchell, D. J., & Brass, M. (2017). Neural coding for instruction-based task sets in human frontoparietal and visual cortex. *Cerebral Cortex*, 27(3), 1891-1905. <https://doi.org/10.1093/cercor/bhw032>
- Muhle-Karbe, P. S., Jiang, J., & Egner, T. (2018). Causal evidence for learning-dependent frontal lobe contributions to cognitive control. *Journal of Neuroscience*, 38(4), 962-973. <https://doi.org/10.1523/JNEUROSCI.1467-17.2017>
- Müller, V. I., Cieslik, E. C., Laird, A. R., Fox, P. T., Radua, J., Mataix-Cols, D., Tench, C. R., Yarkoni, T., Nichols, T. E., Turkeltaub, P. E., Wager, T. D., & Eickhoff, S. B. (2018). Ten simple rules for neuroimaging meta-analysis. *Neuroscience and Biobehavioral Reviews*, 84(November 2017), 151–161. <https://doi.org/10.1016/j.neubiorev.2017.11.012>
- Nee, D. E., & D'Esposito, M. (2016). The hierarchical organization of the lateral prefrontal cortex. *eLife*, 5, e12112. <https://doi.org/10.7554/eLife.12112.002>
- Nee, D. E., Brown, J. W., Askren, M. K., Berman, M. G., Demiralp, E., Krawitz, A., & Jonides, J. (2013). A meta-Analysis of executive components of working memory. *Cerebral Cortex*, 23(2), 264–282. <https://doi.org/10.1093/cercor/bhs007>
- Nee, D. E., Jahn, A., & Brown, J. W. (2014). Prefrontal cortex organization: Dissociating effects of temporal abstraction, relational abstraction, and integration with fMRI. *Cerebral Cortex*, 24(9), 2377–2387. <https://doi.org/10.1093/cercor/bht091>
- Neggers, S. F., Huijbers, W., Vrijlandt, C. M., Vlaskamp, B. N., Schutter, D. J., & Kenemans, J. L. (2007). TMS pulses on the frontal eye fields break coupling between visuospatial attention and eye movements. *Journal of neurophysiology*, 98(5), 2765-2778. <https://doi.org/10.1152/jn.00357.2007>
- Neggers, S. F. W., van Diepen, R. M., Zandbelt, B. B., Vink, M., Mandl, R. C. W., & Gutteling, T. P. (2012). A functional and structural investigation of the human fronto-basal volitional saccade network. *PLoS ONE*, 7(1). <https://doi.org/10.1371/journal.pone.0029517>
- Neggers, S. F. W., Zandbelt, B. B., Schall, M. S., & Schall, J. D. (2015). Comparative diffusion tractography of corticostriatal motor pathways reveals differences between humans and macaques. *Journal of Neurophysiology*, 113(7), 2164–2172. <https://doi.org/10.1152/jn.00569.2014>

- Neubert, F. X., Mars, R. B., Thomas, A. G., Sallet, J., & Rushworth, M. F. S. (2014). Comparison of Human Ventral Frontal Cortex Areas for Cognitive Control and Language with Areas in Monkey Frontal Cortex. *Neuron*, 81(3), 700–713. <https://doi.org/10.1016/j.neuron.2013.11.012>
- Ngo, G. H., Eickhoff, S. B., Nguyen, M., Sevinc, G., Fox, P. T., Spreng, R. N., & Yeo, B. T. (2019). Beyond consensus: embracing heterogeneity in curated neuroimaging meta-analysis. *NeuroImage*, 200, 142–158. <https://doi.org/10.1016/j.neuroimage.2019.06.037>
- Niso, G., Tadel, F., Bock, E., Cousineau, M., Santos, A., & Baillet, S. (2019). Brainstorm pipeline analysis of resting-state data from the open MEG archive. *Frontiers in neuroscience*, 13, 284. <https://doi.org/10.3389/fnins.2019.00284>
- Nobre, A. C. (2001). The attentive homunculus: now you see it, now you don't. *Neuroscience & Biobehavioral Reviews*, 25(6), 477–496. [https://doi.org/10.1016/S0149-7634\(01\)00028-8](https://doi.org/10.1016/S0149-7634(01)00028-8)
- Norman, D. A., & Shallice, T. (1986). Attention to action. In *Consciousness and self-regulation* (pp. 1–18). Springer, Boston, MA. https://doi.org/10.1007/978-1-4757-0629-1_1
- Noyce, A. L., Cestero, N., Michalka, S. W., Shinn-Cunningham, B. G., & Somers, D. C. (2017). Sensory-biased and multiple-demand processing in human lateral frontal cortex. *Journal of Neuroscience*, 37(36), 8755–8766. <https://doi.org/10.1523/JNEUROSCI.0660-17.2017>
- Numssen, O., Bzdok, D., & Hartwigsen, G. (2021). Functional specialization within the inferior parietal lobes across cognitive domains. *elife*, 10, e63591. <https://doi.org/10.1101/2020.07.01.181602>
- Oberauer, K. (2019). Working memory and attention—A conceptual analysis and review. *Journal of cognition*, 2(1). <http://doi.org/10.5334/joc.58>
- Olivers, C. N. (2008). Interactions between visual working memory and visual attention. *Frontiers in Bioscience*, 13(3), 1182–1191. <https://doi.org/10.2741/2754>
- Ono, M., Kubik, S., & Abernathy, C. D. Atlas of the cerebral sulci (1990). New York. NY: Thieme Medical Publishers.
- Osher, D. E., Brissenden, J. A., & Somers, D. C. (2019). Predicting an individual's dorsal attention network activity from functional connectivity fingerprints. *Journal of Neurophysiology*, 122(1), 232–240. <https://doi.org/10.1152/jn.00174.2019>
- Osher, D. E., Saxe, R. R., Koldewyn, K., Gabrieli, J. D. E., Kanwisher, N., & Saygin, Z. M. (2016). Structural Connectivity Fingerprints Predict Cortical Selectivity for

-
- Multiple Visual Categories across Cortex. *Cerebral Cortex*, 26(4), 1668–1683. <https://doi.org/10.1093/cercor/bhu303>
- Owen, A. M., Stern, C. E., Look, R. B., Tracey, I., Rosen, B. R., & Petrides, M. (1998). Functional organization of spatial and nonspatial working memory processing within the human lateral frontal cortex. *Proceedings of the National Academy of Sciences*, 95(13), 7721–7726. <https://doi.org/10.1073/pnas.95.13.7721>
- O’Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature*, 401(6753), 584–587. <https://doi.org/10.1038/44134>
- O’Reilly, R. C. (2010). The what and how of prefrontal cortical organization. *Trends in Neurosciences*, 33(8), 355–361. <https://doi.org/10.1016/j.tins.2010.05.002>
- Page, M. J., McKenzie, J. E., Bossuyt, P. M., Boutron, I., Hoffmann, T. C., Mulrow, C. D., Shamseer, L., Tetzlaff, J. M., Akl, E. A., Brennan, S. E., Chou, R., Glanville, J., Grimshaw, J. M., Hróbjartsson, A., Lalu, M. M., Li, T., Loder, E. W., Mayo-Wilson, E., McDonald, S., ... Moher, D. (2021). The PRISMA 2020 statement: An updated guideline for reporting systematic reviews. *The BMJ*, 372. <https://doi.org/10.1136/bmj.n71>
- Parlatini, V., Radua, J., Dell’Acqua, F., Leslie, A., Simmons, A., Murphy, D. G., ... & de Schotten, M. T. (2017). Functional segregation and integration within fronto-parietal networks. *Neuroimage*, 146, 367–375. <https://doi.org/10.1016/j.neuroimage.2016.08.031>
- Parvathaneni, P., Lyu, I., Huo, Y., Rogers, B. P., Schilling, K. G., Nath, V., Blaber, J. A., Hainline, A. E., Anderson, A. W., Woodward, N. D., & Landman, B. A. (2019). Improved gray matter surface based spatial statistics in neuroimaging studies. *Magnetic Resonance Imaging*, 61(March), 285–295. <https://doi.org/10.1016/j.mri.2019.05.016>
- Pashler, H. (1994). Dual-task interference in simple tasks: data and theory. *Psychological bulletin*, 116(2), 220. <https://doi.org/10.1037/0033-2909.116.2.220>
- Passingham, R. E., & Lau, H. (2022). Do we understand the prefrontal cortex? *Brain Structure and Function*, 0123456789. <https://doi.org/10.1007/s00429-022-02587-7>
- Passingham, R. E., Stephan, K. E., & Kötter, R. (2002). The anatomical basis of functional localization in the cortex. *Nature Reviews Neuroscience*, 3(8), 606–616. <https://doi.org/10.1038/nrn893>
- Paus, T. (1996). Location and function of the human frontal eye-field: a selective review. *Neuropsychologia*, 34(6), 475–483. [https://doi.org/10.1016/0028-3932\(95\)00134-4](https://doi.org/10.1016/0028-3932(95)00134-4)

- Peelen, M. V., & Downing, P. E. (2005). Selectivity for the human body in the fusiform gyrus. *Journal of Neurophysiology*, 93(1), 603–608. <https://doi.org/10.1152/jn.00513.2004>
- Penfield, W., & Rasmussen, T. (1950). The cerebral cortex of man; a clinical study of localization of function. Macmillan.
- Pestilli, F., Yeatman, J. D., Rokem, A., Kay, K. N., & Wandell, B. A. (2014). Evaluation and statistical inference for human connectomes. *Nature Methods*, 11(10), 1058–1063. <https://doi.org/10.1038/nmeth.3098>
- Petit, L., & Pouget, P. (2019). The comparative anatomy of frontal eye fields in primates. *Cortex*, 118, 51–64. <https://doi.org/10.1016/j.cortex.2019.02.023>
- Petrides, M., & Pandya, D. N. (1999). Dorsolateral prefrontal cortex: comparative cytoarchitectonic analysis in the human and the macaque brain and corticocortical connection patterns. *European Journal of Neuroscience*, 11(3), 1011–1036. <https://doi.org/10.1046/j.1460-9568.1999.00518.x>
- Petrides, M., & Pandya, D. N. (2002). Comparative cytoarchitectonic analysis of the human and the macaque ventrolateral prefrontal cortex and corticocortical connection patterns in the monkey. *European Journal of Neuroscience*, 16(2), 291–310. <https://doi.org/10.1046/j.1460-9568.2001.02090.x>
- Petrides, M., Tomaiuolo, F., Yeterian, E. H., & Pandya, D. N. (2012). The prefrontal cortex: comparative architectonic organization in the human and the macaque monkey brains. *Cortex*, 48(1), 46–57. <https://doi.org/10.1016/j.cortex.2011.07.002>
- Petrides, M. (2005). Lateral prefrontal cortex: Architectonic and functional organization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360(1456), 781–795. <https://doi.org/10.1098/rstb.2005.1631>
- Petrides, M. (2018). *Atlas of the morphology of the human cerebral cortex on the average MNI brain*. Academic Press.
- Pierce, J. E., & McDowell, J. E. (2015). Modulation of cognitive control levels via manipulation of saccade trial-type probability assessed with event-related BOLD fMRI. *Journal of Neurophysiology*, 115(2), 763–772. <https://doi.org/10.1152/jn.00776.2015>
- Pierce, J. E., & McDowell, J. E. (2017). Contextual effects on cognitive control and BOLD activation in single versus mixed saccade tasks. *Brain and Cognition*, 115, 12–20. <https://doi.org/10.1016/j.bandc.2017.03.003>

-
- Pierce, J. E., Saj, A., & Vuilleumier, P. (2019). Differential parietal activations for spatial remapping and saccadic control in a visual memory task. *Neuropsychologia*, 131(May), 129–138. <https://doi.org/10.1016/j.neuropsychologia.2019.05.010>
- Pierrot-Deseilligny, C., Ploner, C. J., Müri, R. M., Gaymard, B., & Rivaud-Péchoix, S. (2002). Effects of cortical lesions on saccadic eye movements in humans. *Annals of the New York Academy of Sciences*, 956, 216–229. <https://doi.org/10.1111/j.1749-6632.2002.tb02821.x>
- Poldrack, R. A. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Sciences*, 10(2), 59–63. <https://doi.org/10.1016/j.tics.2005.12.004>
- Poldrack, R. A. (2011). Inferring mental states from neuroimaging data: From reverse inference to large-scale decoding. *Neuron*, 72(5), 692–697. <https://doi.org/10.1016/j.neuron.2011.11.001>
- Popov, T., Kastner, S., & Jensen, O. (2017). FEF-controlled alpha delay activity precedes stimulus-induced gamma-band activity in visual cortex. *Journal of Neuroscience*, 37(15), 4117–4127. <https://doi.org/10.1523/JNEUROSCI.3015-16.2017>
- Posner, M. I. (1980). Orienting of attention. *Quarterly journal of experimental psychology*, 32(1), 3–25. <https://doi.org/10.1080/00335558008248231>
- Posner, M. I., Snyder, C. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General*, 109(2), 160–174. <https://doi.org/10.1037/0096-3445.109.2.160>
- Preuss, T. M., & Wise, S. P. (2022). Evolution of prefrontal cortex. *Neuropsychopharmacology*, 47(1), 3–19. <https://doi.org/10.1038/s41386-021-01076-5>
- Quentin, R., Chanes, L., Vernet, M., & Valero-Cabré, A. (2015). Fronto-parietal anatomical connections influence the modulation of conscious visual perception by high-beta frontal oscillatory activity. *Cerebral cortex*, 25(8), 2095–2101. <https://doi.org/10.1093/cercor/bhu014>
- Rainer, G., Asaad, W. F., & Miller, E. K. (1998). Selective representation of relevant information by neurons in the primate prefrontal cortex. *Nature*, 393(6685), 577–579. <https://doi.org/10.1038/31235>
- Rajan, A., Meyyappan, S., Liu, Y., Samuel, I. B. H., Nandi, B., Mangun, G. R., & Ding, M. (2021). The Microstructure of Attentional Control in the Dorsal Attention Network. *Journal of Cognitive Neuroscience*, 33(6), 965–983. https://doi.org/10.1162/jocn_a_01710

- Rao, S. C., Rainer, G., & Miller, E. K. (1997). Integration of what and where in the primate prefrontal cortex. *Science*, 276(5313), 821-824. <https://doi.org/10.1126/science.276.5313.821>
- Reid, A. T., Bzdok, D., Genon, S., Langner, R., Müller, V. I., Eickhoff, C. R., Hoffstaedter, F., Cieslik, E. C., Fox, P. T., Laird, A. R., Amunts, K., Caspers, S., & Eickhoff, S. B. (2016). ANIMA: A data-sharing initiative for neuroimaging meta-analyses. *NeuroImage*, 124, 1245–1253. <https://doi.org/10.1016/j.neuroimage.2015.07.060>
- Reveley, C., Seth, A. K., Pierpaoli, C., Silva, A. C., Yu, D., Saunders, R. C., Leopold, D. A., & Ye, F. Q. (2015). Superficial white matter fiber systems impede detection of long-range cortical connections in diffusion MR tractography. *Proceedings of the National Academy of Sciences of the United States of America*, 112(21), E2820–E2828. <https://doi.org/10.1073/pnas.1418198112>
- Rigotti, M., Barak, O., Warden, M. R., Wang, X. J., Daw, N. D., Miller, E. K., & Fusi, S. (2013). The importance of mixed selectivity in complex cognitive tasks. *Nature*, 497(7451), 585–590. <https://doi.org/10.1038/nature12160>
- Riley, M. R., Qi, X. L., & Constantinidis, C. (2017). Functional specialization of areas along the anterior–posterior axis of the primate prefrontal cortex. *Cerebral Cortex*, 27(7), 3683-3697. <https://doi.org/10.1093/cercor/bhw190>
- Rilling, J. K., Glasser, M. F., Preuss, T. M., Ma, X., Zhao, T., Hu, X., & Behrens, T. E. J. (2008). The evolution of the arcuate fasciculus revealed with comparative DTI. *Nature Neuroscience*, 11(4), 426–428. <https://doi.org/10.1038/nn2072>
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25(1), 31-40. [https://doi.org/10.1016/0028-3932\(87\)90041-8](https://doi.org/10.1016/0028-3932(87)90041-8)
- Roberts, J. A., Perry, A., Lord, A. R., Roberts, G., Mitchell, P. B., Smith, R. E., Calamante, F., & Breakspear, M. (2016). The contribution of geometry to the human connectome. *NeuroImage*, 124, 379–393. <https://doi.org/10.1016/j.neuroimage.2015.09.009>
- Robinson, E. C., Jbabdi, S., Glasser, M. F., Andersson, J., Burgess, G. C., Harms, M. P., ... & Jenkinson, M. (2014). MSM: a new flexible framework for Multimodal Surface Matching. *Neuroimage*, 100, 414-426. <https://doi.org/10.1016/j.neuroimage.2014.05.069>
- Robinson, J. L., Laird, A. R., Glahn, D. C., Lovallo, W. R., & Fox, P. T. (2010). Metaanalytic connectivity modeling: delineating the functional connectivity of the

-
- human amygdala. *Human brain mapping*, 31(2), 173-184.
<https://doi.org/10.1002/hbm.20854>
- Robinson, E. C., Garcia, K., Glasser, M. F., Chen, Z., Coalson, T. S., Makropoulos, A., Bozek, J., Wright, R., Schuh, A., Webster, M., Hutter, J., Price, A., Cordero Grande, L., Hughes, E., Tusor, N., Bayly, P. V., Van Essen, D. C., Smith, S. M., Edwards, A. D., ... Rueckert, D. (2018). Multimodal surface matching with higher-order smoothness constraints. *NeuroImage*, 167(October 2017), 453–465.
<https://doi.org/10.1016/j.neuroimage.2017.10.037>
- Roine, T., Jeurissen, B., Perrone, D., Aelterman, J., Leemans, A., Philips, W., & Sijbers, J. (2014). Isotropic non-white matter partial volume effects in constrained spherical deconvolution. *Frontiers in Neuroinformatics*, 8(MAR), 1–9.
<https://doi.org/10.3389/fninf.2014.00028>
- Romanski, L. M. (2004). Domain specificity in the primate prefrontal cortex. *Cognitive, Affective, & Behavioral Neuroscience*, 4(4), 421–429.
<https://doi.org/10.3758/CABN.4.4.421>
- Ronconi, L., Basso, D., Gori, S., & Facoetti, A. (2014). TMS on right frontal eye fields induces an inflexible focus of attention. *Cerebral Cortex*, 24(2), 396-402.
<https://doi.org/10.1093/cercor/bhs319>
- Rosano, C., Sweeney, J. A., Melchitzky, D. S., & Lewis, D. A. (2003). The human precentral sulcus: Chemoarchitecture of a region corresponding to the frontal eye fields. *Brain Research*, 972(1–2), 16–30.
[https://doi.org/10.1016/S0006-8993\(03\)02431-4](https://doi.org/10.1016/S0006-8993(03)02431-4)
- Rose, J. E., & Woolsey, C. N. (1948). The orbitofrontal cortex and its connections with the mediodorsal nucleus in rabbit, sheep and cat. *Research publications - Association for Research in Nervous and Mental Disease*, 27 (1 vol.), 210–232.
- Rosen, B. Q., & Halgren, E. (2021). A Whole-Cortex Probabilistic Diffusion Tractography Connectome. *Eneuro*, 8(1), ENEURO-0416.
<https://doi.org/10.1523/ENEURO.0416-20.2020>
- Roth, J. K., Serences, J. T., & Courtney, S. M. (2006). Neural system for controlling the contents of object working memory in humans. *Cerebral Cortex*, 16(11), 1595–1603. <https://doi.org/10.1093/cercor/bhj096>
- Rottschy, C., Langner, R., Dogan, I., Reetz, K., Laird, A. R., Schulz, J. B., ... & Eickhoff, S. B. (2012). Modelling neural correlates of working memory: a coordinate-based meta-analysis. *Neuroimage*, 60(1), 830-846.
<https://doi.org/10.1016/j.neuroimage.2011.11.050>

- Ruff, C. C., Blankenburg, F., Bjoertomt, O., Bestmann, S., Freeman, E., Haynes, J. D., ... & Driver, J. (2006). Concurrent TMS-fMRI and psychophysics reveal frontal influences on human retinotopic visual cortex. *Current Biology*, 16(15), 1479-1488. <https://doi.org/10.1016/j.cub.2006.06.057>
- Ruland, S. H., Palomero-Gallagher, N., Hoffstaedter, F., Eickhoff, S. B., Mohlberg, H., & Amunts, K. (2022). The inferior frontal sulcus: Cortical segregation, molecular architecture and function. *Cortex*, 153, 235-256. <https://doi.org/10.1016/j.cortex.2022.03.019>
- Sallet, J., Mars, R. B., Noonan, M. P., Neubert, F.-X., Jbabdi, S., O'Reilly, J. X., Filippini, N., Thomas, A. G., & Rushworth, M. F. (2013). The Organization of Dorsal Frontal Cortex in Humans and Macaques. *Journal of Neuroscience*, 33(30), 12255–12274. <https://doi.org/10.1523/JNEUROSCI.5108-12.2013>
- Salvia, E., Harvey, M., Nazarian, B., & Grosbras, M. H. (2020). Social perception drives eye-movement related brain activity: Evidence from pro- and anti-saccades to faces. *Neuropsychologia*, 139(March 2019), 107360. <https://doi.org/10.1016/j.neuropsychologia.2020.107360>
- Sani, I., McPherson, B. C., Stemmann, H., Pestilli, F., & Freiwald, W. A. (2019). Functionally defined white matter of the macaque monkey brain reveals a dorso-ventral attention network. *ELife*, 8, 1–21. <https://doi.org/10.7554/eLife.40520>
- Sani, I., Stemmann, H., Caron, B., Bullock, D., Stemmler, T., Fahle, M., Pestilli, F., & Freiwald, W. A. (2021). The human endogenous attentional control network includes a ventro-temporal cortical node. *Nature Communications*, 12(1), 1–16. <https://doi.org/10.1038/s41467-020-20583-5>
- Sarwar, T., Ramamohanarao, K., & Zalesky, A. (2021). A critical review of connectome validation studies. *NMR in Biomedicine*, 34(12), 1–18. <https://doi.org/10.1002/nbm.4605>
- Saslow, M. G. (1967). Effects of components of displacement-step stimuli upon latency for saccadic eye movement. *Journal of the Optical Society of America*, 57(8), 1024–1029. <https://doi.org/10.1364/JOSA.57.001024>
- Saygin, A. P., & Sereno, M. I. (2008). Retinotopy and attention in human occipital, temporal, parietal, and frontal cortex. *Cerebral Cortex*, 18(9), 2158–2168. <https://doi.org/10.1093/cercor/bhm242>
- Saygin, Z. M., Osher, D. E., Koldewyn, K., Reynolds, G., Gabrieli, J. D. E., & Saxe, R. R. (2012). Anatomical connectivity patterns predict face selectivity in the fusiform gyrus. *Nature Neuroscience*, 15(2), 321–327. <https://doi.org/10.1038/nn.3001>

-
- Scalaidhe, S. P. Ó., Wilson, F. A., & Goldman-Rakic, P. S. (1997). Areal segregation of face-processing neurons in prefrontal cortex. *Science*, 278(5340), 1135-1138. <https://doi.org/10.1126/science.278.5340.1135>
- Scalaidhe, S. P. Ó., Wilson, F. A. W., & Goldman-Rakic, P. S. (1999). Face-selective neurons during passive viewing and working memory performance of rhesus monkeys: evidence for intrinsic specialization of neuronal coding. *Cerebral Cortex*, 9(5), 459–475. <https://doi.org/10.1093/cercor/9.5.459>
- Schall, J. D., Morel, A., King, D. J., & Bullier, J. (1995). Topography of visual cortex connections with frontal eye field in macaque: convergence and segregation of processing streams. *Journal of Neuroscience*, 15(6), 4464-4487. <https://doi.org/10.1523/JNEUROSCI.15-06-04464.1995>
- Schall, J. D., Zinke, W., Cosman, J. D., Schall, M. S., Paré, M., & Pouget, P. (2020). On the evolution of the frontal eye field: comparisons of monkeys, apes, and humans. In *Evolutionary neuroscience* (pp. 861-890). Academic Press. <https://doi.org/10.1016/b978-0-12-820584-6.00036-2>
- Schall, J. D. (2015). Visuomotor functions in the frontal lobe. *Annual Review of Vision Science*, 1, 469-498. <https://doi.org/10.1146/annurev-vision-082114-035317>
- Schall, J. D., & Hanes, D. P. (1998). Neural mechanisms of selection and control of visually guided eye movements. *Neural Networks*, 11(7-8), 1241-1251. [https://doi.org/10.1016/S0893-6080\(98\)00059-8](https://doi.org/10.1016/S0893-6080(98)00059-8)
- Scheperjans, F., Eickhoff, S. B., Hömke, L., Mohlberg, H., Hermann, K., Amunts, K., & Zilles, K. (2008). Probabilistic maps, morphometry, and variability of cytoarchitectonic areas in the human superior parietal cortex. *Cerebral Cortex*, 18(9), 2141–2157. <https://doi.org/10.1093/cercor/bhm241>
- Scheperjans, F., Hermann, K., Eickhoff, S. B., Amunts, K., Schleicher, A., & Zilles, K. (2008). Observer-independent cytoarchitectonic mapping of the human superior parietal cortex. *Cerebral Cortex*, 18(4), 846–867. <https://doi.org/10.1093/cercor/bhm116>
- Schilling, K., Gao, Y., Janve, V., Stepniewska, I., Landman, B. A., & Anderson, A. W. (2018). Confirmation of a gyral bias in diffusion MRI fiber tractography. *Human Brain Mapping*, 39(3), 1449–1466. <https://doi.org/10.1002/hbm.23936>
- Schmahmann, J. D., & Pandya, D. N. (2006). *Fiber Pathways of the Brain*. Oxford University Press.
- Schmitt, O., Modersitzki, J., Heldmann, S., Wirtz, S., Hömke, L., Heide, W., ... & Wree, A. (2005). Three-dimensional cytoarchitectonic analysis of the posterior bank of

- the human precentral sulcus. *Anatomy and embryology*, 210(5), 387-400. <https://doi.org/10.1007/s00429-005-0030-8>
- Schon, K., Tinaz, S., Somers, D. C., & Stern, C. E. (2008). Delayed match to object or place: An event-related fMRI study of short-term stimulus maintenance and the role of stimulus pre-exposure. *NeuroImage*, 39(2), 857–872. <https://doi.org/10.1016/j.neuroimage.2007.09.023>
- Schwedhelm, P., Baldauf, D., & Treue, S. (2017). Electrical stimulation of macaque lateral prefrontal cortex modulates oculomotor behavior indicative of a disruption of top-down attention. *Scientific Reports*, 7(1), 1–10. <https://doi.org/10.1038/s41598-017-18153-9>
- Schwedhelm, P., Baldauf, D., & Treue, S. (2020). The lateral prefrontal cortex of primates encodes stimulus colors and their behavioral relevance during a match-to-sample task. *Scientific Reports*, 10(1), 1–12. <https://doi.org/10.1038/s41598-020-61171-3>
- Serences, J. T., & Boynton, G. M. (2007). Feature-based attentional modulations in the absence of direct visual stimulation. *Neuron*, 55(2), 301-312. <https://doi.org/10.1016/j.neuron.2007.06.015>
- Serences, J. T., Schwarzbach, J., Courtney, S. M., Golay, X., & Yantis, S. (2004). Control of object-based attention in human cortex. *Cerebral Cortex*, 14(12), 1346–1357. <https://doi.org/10.1093/cercor/bhh095>
- Serences, J. T. (2016). Neural mechanisms of information storage in visual short-term memory. *Vision Research*, 128, 53–67. <https://doi.org/10.1016/j.visres.2016.09.010>
- Sereno, M. I., Dale, A. M., Reppas, J. B., Kwong, K. K., Belliveau, J. W., Brady, T. J., ... & Tootell, R. B. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*, 268(5212), 889-893. <https://doi.org/10.1126/science.7754376>
- Seth, A. K., Barrett, A. B., & Barnett, L. (2015). Granger causality analysis in neuroscience and neuroimaging. *Journal of Neuroscience*, 35(8), 3293-3297. <https://doi.org/10.1523/JNEUROSCI.4399-14.2015>
- Shastin, D., Genc, S., Parker, G. D., Koller, K., Tax, C. M. W., Evans, J., Hamandi, K., Gray, W. P., Jones, D. K., & Chamberland, M. (2022). Surface-based tracking for short association fibre tractography. *NeuroImage*, 260(April 2021), 119423. <https://doi.org/10.1016/j.neuroimage.2022.119423>
- Shulman, G. L., Astafiev, S. V., Franke, D., Pope, D. L., Snyder, A. Z., McAvoy, M. P., & Corbetta, M. (2009). Interaction of stimulus-driven reorienting and expectation in ventral and dorsal frontoparietal and basal ganglia-cortical networks. *Journal of*

- Sims, S. A., Demirayak, P., Cedotal, S., & Visscher, K. M. (2021). Frontal cortical regions associated with attention connect more strongly to central than peripheral V1. *NeuroImage*, 238(June), 118246. <https://doi.org/10.1016/j.neuroimage.2021.118246>
- Slagter, H. A., Giesbrecht, B., Kok, A., Weissman, D. H., Kenemans, J. L., Woldorff, M. G., & Mangun, G. R. (2007). fMRI evidence for both generalized and specialized components of attentional control. *Brain research*, 1177, 90-102. <https://doi.org/10.1016/j.brainres.2007.07.097>
- Smith, R. E., Tournier, J. D., Calamante, F., & Connelly, A. (2012). Anatomically-constrained tractography: Improved diffusion MRI streamlines tractography through effective use of anatomical information. *NeuroImage*, 62(3), 1924–1938. <https://doi.org/10.1016/j.neuroimage.2012.06.005>
- Smith, R. E., Tournier, J. D., Calamante, F., & Connelly, A. (2015). SIFT2: Enabling dense quantitative assessment of brain white matter connectivity using streamlines tractography. *NeuroImage*, 119, 338–351. <https://doi.org/10.1016/j.neuroimage.2015.06.092>
- Sneve, M. H., Magnussen, S., Alnæs, D., Endestad, T., & D'Esposito, M. (2013). Top-down modulation from inferior frontal junction to FEFs and intraparietal sulcus during short-term memory for visual features. *Journal of Cognitive Neuroscience*, 25(11), 1944–1956. https://doi.org/10.1162/jocn_a_00426
- Sotiropoulos, S. N., Hernández-Fernández, M., Vu, A. T., Andersson, J. L., Moeller, S., Yacoub, E., Lenglet, C., Ugurbil, K., Behrens, T. E. J., & Jbabdi, S. (2016). Fusion in diffusion MRI for improved fibre orientation estimation: An application to the 3T and 7T data of the Human Connectome Project. *NeuroImage*, 134, 396–409. <https://doi.org/10.1016/j.neuroimage.2016.04.014>
- Sotiropoulos, S. N., Jbabdi, S., Xu, J., Andersson, J. L., Moeller, S., Auerbach, E. J., Glasser, M. F., Hernandez, M., Sapiro, G., Jenkinson, M., Feinberg, D. A., Yacoub, E., Lenglet, C., Sprague, T. C., & Serences, J. T. (2013). Attention modulates spatial priority maps in the human occipital, parietal and frontal cortices. *Nature Neuroscience*, 16(12), 1879–1887. <https://doi.org/10.1038/nn.3574>
- Sporns, O., Tononi, G., & Kötter, R. (2005). The human connectome: A structural description of the human brain. *PLoS Computational Biology*, 1(4), 0245–0251. <https://doi.org/10.1371/journal.pcbi.0010042>

- Sprague, T. C., & Serences, J. T. (2013). Attention modulates spatial priority maps in the human occipital, parietal and frontal cortices. *Nature Neuroscience*, 16(12), 1879–1887. <https://doi.org/10.1038/nn.3574>
- Sreenivasan, K. K., Curtis, C. E., & D’Esposito, M. (2014). Revisiting the role of persistent neural activity during working memory. *Trends in Cognitive Sciences*, 18(2), 82–89. <https://doi.org/10.1016/j.tics.2013.12.001>
- Sreenivasan, K. K., Gratton, C., Vytlačil, J., & D’Esposito, M. (2014). Evidence for working memory storage operations in perceptual cortex. *Cognitive, Affective and Behavioral Neuroscience*, 14(1), 117–128. <https://doi.org/10.3758/s13415-013-0246-7>
- Srimal, R., & Curtis, C. E. (2008). Persistent neural activity during the maintenance of spatial position in working memory. *Neuroimage*, 39(1), 455–468. <https://doi.org/10.1016/j.neuroimage.2007.08.040>
- Stanton, G. B., Bruce, C. J., & Goldberg, M. E. (1993). Topography of projections to the frontal lobe from the macaque frontal eye fields. *Journal of Comparative Neurology*, 330(2), 286–301. <https://doi.org/10.1002/cne.903300209>
- Stelzel, C., Basten, U., & Fiebach, C. J. (2011). Functional connectivity separates switching operations in the posterior lateral frontal cortex. *Journal of Cognitive Neuroscience*, 23(11), 3529–3539. https://doi.org/10.1162/jocn_a_00062
- Stiers, P., & Goulas, A. (2018). Functional connectivity of task context representations in prefrontal nodes of the multiple demand network. *Brain Structure and Function*, 223(5), 2455–2473. <https://doi.org/10.1007/s00429-018-1638-9>
- St-Onge, E., Al-Sharif, N., Girard, G., Theaud, G., & Descoteaux, M. (2021). Cortical Surfaces Integration with Tractography for Structural Connectivity Analysis. *Brain Connectivity*, 11(7), 505–517. <https://doi.org/10.1089/brain.2020.0930>
- St-Onge, E., Daducci, A., Girard, G., & Descoteaux, M. (2018). Surface-enhanced tractography (SET). *NeuroImage*, 169(December 2017), 524–539. <https://doi.org/10.1016/j.neuroimage.2017.12.036>
- Störmer, V. S., & Alvarez, G. A. (2014). Feature-based attention elicits surround suppression in feature space. *Current Biology*, 24(17), 1985–1988. <https://doi.org/10.1016/j.cub.2014.07.030>
- Sundermann, B., & Pfleiderer, B. (2012). Functional connectivity profile of the human inferior frontal junction: Involvement in a cognitive control network. *BMC Neuroscience*, 13(1). <https://doi.org/10.1186/1471-2202-13-119>

-
- Sylvester, C. Y. C., Wager, T. D., Lacey, S. C., Hernandez, L., Nichols, T. E., Smith, E. E., & Jonides, J. (2003). Switching attention and resolving interference: fMRI measures of executive functions. *Neuropsychologia*, 41(3), 357-370. [https://doi.org/10.1016/S0028-3932\(02\)00167-7](https://doi.org/10.1016/S0028-3932(02)00167-7)
- Szczepanski, S. M., & Knight, R. T. (2014). Insights into Human Behavior from Lesions to the Prefrontal Cortex. *Neuron*, 83(5), 1002–1018. <https://doi.org/10.1016/j.neuron.2014.08.011>
- Szczepanski, S. M., Crone, N. E., Kuperman, R. A., Augustine, K. I., Parviz, J., & Knight, R. T. (2014). Dynamic changes in phase-amplitude coupling facilitate spatial attention control in fronto-parietal cortex. *PLoS Biology*, 12(8). <https://doi.org/10.1371/journal.pbio.1001936>
- Szczepanski, S. M., Pinsk, M. A., Douglas, M. M., Kastner, S., & Saalmann, Y. B. (2013). Functional and structural architecture of the human dorsal frontoparietal attention network. *Proceedings of the National Academy of Sciences*, 110(39), 15806-15811. <https://doi.org/10.1073/pnas.1313903110>
- Tabarelli, D., Keitel, C., Gross, J., & Baldauf, D. (2020). Spatial attention enhances cortical tracking of quasi-rhythmic visual stimuli. *NeuroImage*, 208, 116444. <https://doi.org/10.1016/j.neuroimage.2019.116444>
- Takemura, H., Caiafa, C. F., Wandell, B. A., & Pestilli, F. (2016). Ensemble Tractography. *PLoS Computational Biology*, 12(2), 1–22. <https://doi.org/10.1371/journal.pcbi.1004692>
- Talairach J, Tournoux P (1988): Co-planar stereotaxic atlas of the human brain: 3-Dimensional proportional system—An approach to cerebral imaging. New York: Thieme.
- Tamber-Rosenau, B. J., Asplund, C. L., & Marois, R. (2018). Functional dissociation of the inferior frontal junction from the dorsal attention network in top-down attentional control. *Journal of neurophysiology*, 120(5), 2498-2512. <https://doi.org/10.1152/jn.00506.2018>
- Tamber-Rosenau, B. J., Dux, P. E., Tombu, M. N., Asplund, C. L., & Marois, R. (2013). Amodal processing in human prefrontal cortex. *Journal of Neuroscience*, 33(28), 11573-11587. <https://doi.org/10.1523/JNEUROSCI.4601-12.2013>
- Tark, K. J., & Curtis, C. E. (2009). Persistent neural activity in the human frontal cortex when maintaining space that is off the map. *Nature Neuroscience*, 12(11), 1463–1468. <https://doi.org/10.1038/nn.2406>
- Tavor, I., Parker Jones, O., Mars, R. B., Smith, S. M., Behrens, T. E., & Jbabdi, S. (2016). Task-free MRI predicts individual differences in brain activity during task

- performance. *Science*, 352(6282), 216–220. <https://doi.org/10.1126/science.aad8127>
- Taylor, P. C., Nobre, A. C., & Rushworth, M. F. (2007). FEF TMS affects visual cortical activity. *Cerebral cortex*, 17(2), 391–399. <https://doi.org/10.1093/cercor/bhj156>
- Tehovnik, E. J., Sommer, M. A., Chou, I. H., Slocum, W. M., & Schiller, P. H. (2000). Eye fields in the frontal lobes of primates. *Brain Research Reviews*, 32(2–3), 413–448. [https://doi.org/10.1016/S0165-0173\(99\)00092-2](https://doi.org/10.1016/S0165-0173(99)00092-2)
- Thakkar, K. N., van den Heiligenberg, F. M. Z., Kahn, R. S., & Neggers, S. F. W. (2014). Frontal-subcortical circuits involved in reactive control and monitoring of gaze. *Journal of Neuroscience*, 34(26), 8918–8929. <https://doi.org/10.1523/JNEUROSCI.0732-14.2014>
- Thompson, K. G., & Bichot, N. P. (2005). A visual salience map in the primate frontal eye field. *Progress in brain research*, 147, 249–262. [https://doi.org/10.1016/S0079-6123\(04\)47019-8](https://doi.org/10.1016/S0079-6123(04)47019-8)
- Thompson, K. G., Bichot, N. P., & Schall, J. D. (1997). Dissociation of visual discrimination from saccade programming in macaque frontal eye field. *Journal of neurophysiology*, 77(2), 1046–1050. <https://doi.org/10.1152/jn.1997.77.2.1046>
- Tibber, M., Saygin, A. P., Grant, S., Melmoth, D., Rees, G., & Morgan, M. (2010). The neural correlates of visuospatial perceptual and oculomotor extrapolation. *PLoS ONE*, 5(3), 1–12. <https://doi.org/10.1371/journal.pone.0009664>
- Tobyne, S. M., Osher, D. E., Michalka, S. W., & Somers, D. C. (2017). Sensory-biased attention networks in human lateral frontal cortex revealed by intrinsic functional connectivity. *Neuroimage*, 162, 362–372. <https://doi.org/10.1016/j.neuroimage.2017.08.020>
- Todd, J. J., Han, S. W., Harrison, S., & Marois, R. (2011). The neural correlates of visual working memory encoding: A time-resolved fMRI study. *Neuropsychologia*, 49(6), 1527–1536. <https://doi.org/10.1016/j.neuropsychologia.2011.01.040>
- Tomassini, V., Jbabdi, S., Klein, J. C., Behrens, T. E. J., Pozzilli, C., Matthews, P. M., Rushworth, M. F. S., & Johansen-Berg, H. (2007). Diffusion-Weighted Imaging Tractography-Based Parcellation of the Human Lateral Premotor Cortex Identifies Dorsal and Ventral Subregions with Anatomical and Functional Specializations. *Journal of Neuroscience*, 27(38), 10259–10269. <https://doi.org/10.1523/JNEUROSCI.2144-07.2007>
- Toro, R., Perron, M., Pike, B., Richer, L., Veillette, S., Pausova, Z., & Paus, T. (2008). Brain size and folding of the human cerebral cortex. *Cerebral Cortex*, 18(10), 2352–2357. <https://doi.org/10.1093/cercor/bhm261>

-
- Tournier, J. D., Calamante, F., & Connelly, A. (2007). Robust determination of the fibre orientation distribution in diffusion MRI: Non-negativity constrained super-resolved spherical deconvolution. *NeuroImage*, 35(4), 1459–1472. <https://doi.org/10.1016/j.neuroimage.2007.02.016>
- Tsao, D. Y., Moeller, S., & Freiwald, W. A. (2008). Comparing face patch systems in macaques and humans. *Proceedings of the National Academy of Sciences of the United States of America*, 105(49), 19514–19519. <https://doi.org/10.1073/pnas.0809662105>
- Tu, P. C., Yang, T. H., Kuo, W. J., Hsieh, J. C., & Su, T. P. (2006). Neural correlates of antisaccade deficits in schizophrenia, an fMRI study. *Journal of Psychiatric Research*, 40(7), 606–612. <https://doi.org/10.1016/j.jpsychires.2006.05.012>
- Turner, R. (2016). Uses, misuses, new uses and fundamental limitations of magnetic resonance imaging in cognitive science. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1705). <https://doi.org/10.1098/rstb.2015.0349>
- Uddin, L. Q., Yeo, B. T. T., & Spreng, R. N. (2019). Towards a Universal Taxonomy of Macro-scale Functional Human Brain Networks. *Brain Topography*, 32(6), 926–942. <https://doi.org/10.1007/s10548-019-00744-6>
- Umarova, R. M., Saur, D., Schnell, S., Kaller, C. P., Vry, M. S., Glauche, V., ... & Weiller, C. (2010). Structural connectivity for visuospatial attention: significance of ventral pathways. *Cerebral cortex*, 20(1), 121–129. <https://doi.org/10.1093/cercor/bhp086>
- van den Heuvel, M. P., de Reus, M. A., Feldman Barrett, L., Scholtens, L. H., Coopmans, F. M., Schmidt, R., ... & Li, L. (2015). Comparison of diffusion tractography and tract-tracing measures of connectivity strength in rhesus macaque connectome. *Human brain mapping*, 36(8), 3064–3075. <https://doi.org/10.1002/hbm.22828>
- van den Heuvel, M. P., de Reus, M. A., Feldman Barrett, L., Scholtens, L. H., Coopmans, F. M. T., Schmidt, R., Preuss, T. M., Rilling, J. K., & Li, L. (2015). Comparison of diffusion tractography and tract-tracing measures of connectivity strength in rhesus macaque connectome. *Human Brain Mapping*, 36(8), 3064–3075. <https://doi.org/10.1002/hbm.22828>
- van Ede, F., & Nobre, A. C. (2023). Turning Attention Inside Out: How Working Memory Serves Behavior. *Annual Review of Psychology*, 74, 137–165. <https://doi.org/10.1146/annurev-psych-021422-041757>
- Van Essen, D. C., Donahue, C. J., Coalson, T. S., Kennedy, H., Hayashi, T., & Glasser, M. F. (2019). Cerebral cortical folding, parcellation, and connectivity in humans, nonhuman primates, and mice. *Proceedings of the National Academy of Sciences of*

- the United States of America*, 116(52), 26173–26180.
<https://doi.org/10.1073/pnas.1902299116>
- Van Essen, D. C., & Drury, H. A. (1997). Structural and functional analyses of human cerebral cortex using a surface-based atlas. *Journal of Neuroscience*, 17(18), 7079–7102. <https://doi.org/10.1523/jneurosci.17-18-07079.1997>
- Van Essen, D. C., Glasser, M. F., Dierker, D. L., Harwell, J., & Coalson, T. (2012). Parcellations and hemispheric asymmetries of human cerebral cortex analyzed on surface-based atlases. *Cerebral Cortex*, 22(10), 2241–2262.
<https://doi.org/10.1093/cercor/bhr291>
- Van Essen, D. C., Jbabdi, S., Sotiropoulos, S. N., Chen, C., Dikranian, K., Coalson, T., ... & Glasser, M. F. (2014). Mapping connections in humans and non-human primates: aspirations and challenges for diffusion imaging. In *Diffusion MRI* (pp. 337–358). Academic Press. <https://doi.org/10.1016/B978-0-12-396460-1.00016-0>
- Van Essen, D. C., Smith, J., Glasser, M. F., Elam, J., Donahue, C. J., Dierker, D. L., ... & Harwell, J. (2017). The brain analysis library of spatial maps and atlases (BALSA) database. *Neuroimage*, 144, 270–274.
<https://doi.org/10.1016/j.neuroimage.2016.04.002>
- Van Essen, D. C., Smith, S. M., Barch, D. M., Behrens, T. E. J., Yacoub, E., & Ugurbil, K. (2013). The WU-Minn Human Connectome Project: An overview. *NeuroImage*, 80, 62–79. <https://doi.org/10.1016/j.neuroimage.2013.05.041>
- Van Essen, D. C., Ugurbil, K., & Behrens, T. E. J. (2013). Advances in diffusion MRI acquisition and processing in the Human Connectome Project. *NeuroImage*, 80, 125–143. <https://doi.org/10.1016/j.neuroimage.2013.05.057>
- Van Essen, D. C. (2007). Cerebral cortical folding patterns in primates: Why they vary and what they signify. *Evolution of Nervous Systems*, 4, 267–276.
<https://doi.org/10.1016/B0-12-370878-8/00344-X>
- VanRullen, R. (2016). Perceptual cycles. *Trends in cognitive sciences*, 20(10), 723–735.
<https://doi.org/10.1016/j.tics.2016.07.006>
- Veniero, D., Gross, J., Morand, S., Duecker, F., Sack, A. T., & Thut, G. (2021). Top-down control of visual cortex by the frontal eye fields through oscillatory realignment. *Nature Communications*, 12(1), 1–13.
<https://doi.org/10.1038/s41467-021-21979-7>
- Verbruggen, F., Aron, A. R., Stevens, M. A., & Chambers, C. D. (2010). Theta burst stimulation dissociates attention and action updating in human inferior frontal cortex. *Proceedings of the National Academy of Sciences*, 107(31), 13966–13971.
<https://doi.org/10.1073/pnas.1001957107>

-
- Vernet, M., Quentin, R., Chanes, L., Mitsumasu, A., & Valero-Cabré, A. (2014). Frontal eye field, where art thou? Anatomy, function, and non-invasive manipulation of frontal regions involved in eye movements and associated cognitive operations. *Frontiers in integrative neuroscience*, 8, 66. <https://doi.org/10.3389/fnint.2014.00066>
- Vezoli, J., Vinck, M., Bosman, C. A., Bastos, A. M., Lewis, C. M., Kennedy, H., & Fries, P. (2021). Brain rhythms define distinct interaction networks with differential dependence on anatomy. *Neuron*, 109(23), 3862-3878.e5. <https://doi.org/10.1016/j.neuron.2021.09.052>
- Vincent, J. L., Kahn, I., Snyder, A. Z., Raichle, M. E., & Buckner, R. L. (2008). Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. *Journal of neurophysiology*, 100(6), 3328-3342. <https://doi.org/10.1152/jn.90355.2008>
- Vincent, J. L., Patel, G. H., Fox, M. D., Snyder, A. Z., Baker, J. T., Van Essen, D. C., Zempel, J. M., Snyder, L. H., Corbetta, M., & Raichle, M. E. (2007). Intrinsic functional architecture in the anaesthetized monkey brain. *Nature*, 447(7140), 83–86. <https://doi.org/10.1038/nature05758>
- Vossel, S., Weidner, R., Driver, J., Friston, K. J., & Fink, G. R. (2012). Deconstructing the architecture of dorsal and ventral attention systems with dynamic causal modeling. *Journal of Neuroscience*, 32(31), 10637-10648. <https://doi.org/10.1523/jneurosci.0414-12.2012>
- Wager, T. D., & Smith, E. E. (2003). Neuroimaging studies of working memory. *Cognitive, Affective, & Behavioral Neuroscience*, 3(4), 255-274. <https://doi.org/10.3758/CABN.3.4.255>
- Walker, A. E. (1940). A cytoarchitectural study of the prefrontal area of the macaque monkey. *Journal of Comparative Neurology*, 73(1), 59-86. <https://doi.org/10.1002/cne.900730106>
- Wang, L., Mruczek, R. E. B., Arcaro, M. J., & Kastner, S. (2015). Probabilistic maps of visual topography in human cortex. *Cerebral Cortex*, 25(10), 3911–3931. <https://doi.org/10.1093/cercor/bhu277>
- Warrington, S., Bryant, K. L., Khrapitchev, A. A., Sallet, J., Charquero-Ballester, M., Douaud, G., Jbabdi, S., Mars, R. B., & Sotiropoulos, S. N. (2020). XTRACT - Standardised protocols for automated tractography in the human and macaque brain. *NeuroImage*, 217(May), 1–15. <https://doi.org/10.1016/j.neuroimage.2020.116923>

- Webster, M. J., Bachevalier, J., & Ungerleider, L. G. (1994). Connections of inferior temporal areas TEO and TE with parietal and frontal cortex in macaque monkeys. *Cerebral cortex*, 4(5), 470-483. <https://doi.org/10.1093/cercor/4.5.470>
- Weiller, C., Reisert, M., Peto, I., Hennig, J., Makris, N., Petrides, M., Rijntjes, M., & Egger, K. (2021). The ventral pathway of the human brain: A continuous association tract system. *NeuroImage*, 234(February), 117977. <https://doi.org/10.1016/j.neuroimage.2021.117977>
- Welker, W. (1990). Why does cerebral cortex fissure and fold? A review of determinants of gyri and sulci. *Cerebral Cortex: comparative structure and evolution of Cerebral Cortex, Part II*, 3-136.
- Wen, X., Yao, L., Liu, Y., & Ding, M. (2012). Causal interactions in attention networks predict behavioral performance. *Journal of Neuroscience*, 32(4), 1284-1292. <https://doi.org/10.1523/JNEUROSCI.2817-11.2012>
- White, B. J., Berg, D. J., Kan, J. Y., Marino, R. A., Itti, L., & Munoz, D. P. (2017). Superior colliculus neurons encode a visual saliency map during free viewing of natural dynamic video. *Nature communications*, 8(1), 1-9. <https://doi.org/10.1038/ncomms14263>
- Wills, K. M., Liu, J., Hakun, J., Zhu, D. C., Hazeltine, E., & Ravizza, S. M. (2017). Neural Mechanisms for the Benefits of Stimulus-Driven Attention. *Cerebral Cortex*, 27(11), 5294–5302. <https://doi.org/10.1093/cercor/bhw308>
- Wilson, F. A., Scalaidhe, S. P., & Goldman-Rakic, P. S. (1993). Dissociation of object and spatial processing domains in primate prefrontal cortex. *Science*, 260(5116), 1955–1958. <https://doi.org/10.1126/science.8316836>
- Xu, T., Nenning, K. H., Schwartz, E., Hong, S. J., Vogelstein, J. T., Goulas, A., ... & Milham, M. P. (2020). Cross-species functional alignment reveals evolutionary hierarchy within the connectome. *NeuroImage*, 223, 117346. <https://doi.org/10.1016/j.neuroimage.2020.117346>
- Xuan B, Mackie MA, Spagna A, et al (2016) The activation of interactive attentional networks. *Neuroimage* 129:308–319. <https://doi.org/10.1016/j.neuroimage.2016.01.017>
- Yeh, C. H., Smith, R. E., Dhollander, T., Calamante, F., & Connelly, A. (2019). Connectomes from streamlines tractography: Assigning streamlines to brain parcellations is not trivial but highly consequential. *NeuroImage*, 199(December 2018), 160–171. <https://doi.org/10.1016/j.neuroimage.2019.05.005>
- Yeo, B. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., ... & Fischl, B. (2011). The organization of the human cerebral cortex estimated by

-
- intrinsic functional connectivity. *Journal of Neurophysiology*, 106(3), 1125. <https://doi.org/10.1152/jn.00338.2011>
- Yeterian, E. H., Pandya, D. N., Tomaiuolo, F., & Petrides, M. (2012). The cortical connectivity of the prefrontal cortex in the monkey brain. *Cortex*, 48(1), 58-81. <https://doi.org/10.1016/j.cortex.2011.03.004>
- Yin S, Deák G, Chen A (2018) Coactivation of cognitive control networks during task switching. *Neuropsychology* 32:31–39. <https://doi.org/10.1037/neu0000406>
- Young, M. P., Hilgetag, C. C., & Scannell, J. W. (2000). On imputing function to structure from the behavioural effects of brain lesions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 355(1393), 147–161. <https://doi.org/10.1098/rstb.2000.0555>
- Zanto, T. P., Rubens, M. T., Bollinger, J., & Gazzaley, A. (2010). Top-down modulation of visual feature processing: the role of the inferior frontal junction. *Neuroimage*, 53(2), 736-745. <https://doi.org/10.1016/j.neuroimage.2010.06.012>
- Zanto, T. P., Rubens, M. T., Thangavel, A., & Gazzaley, A. (2011). Causal role of the prefrontal cortex in top-down modulation of visual processing and working memory. *Nature neuroscience*, 14(5), 656. <https://doi.org/10.1038/nn.2773>
- Zelinsky, G. J., & Bisley, J. W. (2015). The what, where, and why of priority maps and their interactions with visual working memory. *Annals of the New York Academy of Sciences*, 1339(1), 154–164. <https://doi.org/10.1111/nyas.12606>
- Zhang, X., Mlynaryk, N., Ahmed, S., Japee, S., & Ungerleider, L. G. (2018). The role of inferior frontal junction in controlling the spatially global effect of feature-based attention in human visual areas. *PLoS Biology*, 16(6), 1–28. <https://doi.org/10.1371/journal.pbio.2005399>
- Zhao, Y., Kuai, S., Zanto, T. P., & Ku, Y. (2020). Neural Correlates Underlying the Precision of Visual Working Memory. *Neuroscience*, 425, 301–311. <https://doi.org/10.1016/j.neuroscience.2019.11.037>
- Zilles, K., & Amunts, K. (2018). Cytoarchitectonic and receptorarchitectonic organization in Broca's region and surrounding cortex. *Current Opinion in Behavioral Sciences*, 21, 93–105. <https://doi.org/10.1016/j.cobeha.2018.02.011>
- Zilles, K., Palomero-Gallagher, N., & Amunts, K. (2013). Development of cortical folding during evolution and ontogeny. *Trends in Neurosciences*, 36(5), 275–284. <https://doi.org/10.1016/j.tins.2013.01.006>

- Zimmermann, M., Mars, R. B., de Lange, F. P., Toni, I., & Verhagen, L. (2018). Is the extrastriate body area part of the dorsal visuomotor stream? *Brain Structure and Function*, 223(1), 31–46. <https://doi.org/10.1007/s00429-017-1469-0>